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7

THE MORPHOLOGY AND BIOLOGY OF *ERNOBIUS MOLLIS* L. (COLEOPTERA—ANOBIIDAE).

By PHYLLIS GARDINER, B.Sc., F.R.E.S.
(*Queen Elizabeth College, University of London*).

Manuscript received 22nd February, 1952.
(Read 3rd December, 1952.)

With 1 Plate and 16 Text-figures.

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INTRODUCTION.

Ernobius mollis L. is a common and widely distributed member of the Anobiidae. It has previously been described in conjunction with related species by many writers, although these descriptions have referred in the main only to external morphology of the imago and late larval stages. In so far as the internal anatomy has been investigated, the studies have been confined to the mid-gut of the larva and of the beetle and to the ovipositor of the female beetle and the aedeagus of the male.

Descriptions of the life-history and biology of the beetle have been given by several authors, but such descriptions have been included in accounts dealing with several related species and are therefore somewhat brief; in several cases also they refer to conditions as they occur in countries other than Great Britain.

Details of the morphology, internal anatomy and biology of *Ernobius mollis* are included in the present paper. These are of interest in comparison with those described previously for the common Anobiidae of economic importance, *Xestobium rufovillosum* Degeer, *Anobium punctatum* Degeer and *Sitodrepa panicea* L. and the similarity in many of the structures mentioned emphasizes the close relationship of *E. mollis* with these species.

Although in itself not a pest of any importance in this country, a study of its life-history shows that *E. mollis* has much in common with the injurious species referred to. At the same time, its habitat allows of its observation with greater ease than does that of the wood-boring species. No doubt more could be learned of certain aspects of its biology which would be equally applicable to the economically important species which it resembles so closely.

LITERATURE.

Descriptions of the imago of *Ernobius mollis* have been given by many writers, including Ratzeburg (1839), Perris (1854), Fowler (1890), Kemner (1915) and Tooke (1945).

Perris (*l.c.*) and Tooke (*l.c.*) give general accounts of the larva and pupa, and Kemner (*l.c.*) and Kelsey (1946) also give brief descriptions of the larva. The most comprehensive account, however, is provided by Parkin (1933); the full grown or nearly full grown larva is described in detail and external features which distinguish the larva from those of other species are noted and figured. Two keys, based on macroscopical and on microscopical features, are provided for the separation of the larvae of wood-boring Anobiidae.

Ernobius mollis is included by Kemner (*l.c.*) in a key to the larvae of four species of the Anobiidae and by Munro (1915) in two keys for the separation of the larvae of the furniture beetles.

Brief accounts of the life-history have been given by several writers, including Perris, Kemner, Tooke, Kelsey and Cann (1938). Trägårdh (1924), reviewing the group classification of the wood-boring Anobiidae according to their habitat, discusses the infestation by *Ernobius mollis* of standing spruce and stored timber.

The larval gut of several species of the Anobiidae has been studied by a number of workers, including Escherich (1900), Heitz (1927), Breitsprecher (1928), Buchner (1930) and Müller (1934), *E. mollis* being included in the species dealt with by Heitz, Breitsprecher and Müller. These investigations were concerned mainly with the symbiotic micro-flora inhabiting the gastric caeca in the mid-gut, and the work relates variously to the histological details of the gastric caeca, the nature of the symbionts they contain and the method by which the symbionts are transmitted from one generation to the next. In pursuance of the latter topic, Breitsprecher gives a detailed account of the ovipositor of the female beetle.

A description of the male genital armature is given by Sharp and Muir (1912) in a comparative account of the male genital tube in the Coleoptera.

SYNONOMY.

According to Pic (1912), the genus *Ernobius* falls into the subfamily Ernobiinae together with the genera *Ochina* and *Xestobium.*

An inherent variability in the adult structure of *Ernobius mollis* has led in the past to much confusion in its nomenclature.

Synonyms include those of *Anobium molle* of the earlier writers, *Liozuom consimile* of Mulsant and Rey and *Ernobius mulsantianus* of Sharp. Confusion in the identification of individual specimens led to a number of new names which, according to Pic (1917), should relate to the variable *Ernobius mollis* L. Considerable controversy existed between authors, new species being named by Sharp and others in virtue of minor differences in the antennae, tarsi and aedeagus. Some of these names were dismissed by Pic (1916) as having been created owing to an exaggeration of the apparent differences.

Two of Sharp's British species are listed at the present time as being varieties of *Ernobius mollis* L., and thus the species is represented in this country by the two varieties, *Ernobius mollis* v. *mulsantianus* Sharp and *Ernobius mollis* v. *reversus* Sharp, the aedeagus of the two varieties being reversed in all their parts.

DISTRIBUTION AND HABITAT.

Ernobius mollis occurs fairly widely throughout the world. Its distribution is Holarctic, with introduction into South Africa, Australia, New Zealand and New Caledonia.

In Europe it is particularly common in the pine forests of Scandinavia, and it is found throughout Great Britain and in Eire.

Apart from the fact that softwoods only are subject to attack, there appears to be little restriction in the host trees. Infestations of the bark of the following species are on record, and doubtless innumerable others are susceptible :

Picea abies (L.) Karsten	Common spruce.
Pinus nigra f. *austriaca* (Hoess) Asch. and Graebn.	Austrian pine.
Pinus radiata D. Don	Monterey pine
Pinus sylvestris Linnaeus	Scots pine.
Pinus pinaster Aiton	Cluster pine.
Pinus canariensis C. Smith	Canary island pine.
Pinus taeda Linnaeus	Loblolly pine.
Larix decidua Miller	Larch.
Pseudotsuga taxifolia (Poiret) Britton	Douglas fir.

The larvae are restricted almost entirely to the bark, but have been noted as working in the pith canals of *Pinus sylvestris* by Perris (1854) and by myself.

Kelsey (1946) states that in young dead trees the larvae are able to tunnel in any part, and that there are records of attack in milled wood to as much as two inches below the bark.

The larvae appear to have an addiction to resin and are frequently found working in close proximity to the resin canals. It is usually stated that only seasoned wood is liable to attack, but it has been found that the beetles will also breed readily in the bark of wood that has only recently been felled.

MATERIAL AND METHODS.

The *Ernobius mollis* material used was gathered from a number of sources. The original culture was obtained from the Forest Products Research Laboratory, from badly infested pit props of Scots pine (*Pinus sylvestris*). Further supplies were obtained from fencing posts and from the lower dead branches of spruce trees (*Picea abies*) and Douglas fir (*Pseudotsuga taxifolia*). A few larvae and pupae were obtained from the dead lower branches of Austrian pine (*Pinus nigra* f. *austriaca*).

All breeding took place under normal laboratory conditions. Isolated pairs of beetles and larvae were kept in waxed cardboard cream cartons. These containers were found to be most satisfactory. The beetles can get a good grip on the surface, and they are able to move about without falling on their backs. The cartons are also convenient to stack in piles. Ventilation holes were cut in the sides and covered with gauze, but this is probably unnecessary as the screw tops are not air-tight.

The beetles were bred in the bark of small, dry pieces of branch, sawn to a length of 1–2 inches. *Picea abies* and *Pseudotsuga taxifolia* were used for the most part. A few were bred on *Pinus nigra* f. *austriaca*, and larvae were also transferred to and reared in larch (*Larix decidua*). Data relating to the life-history up to the onset of pupation were obtained from cultures bred in this way. For the study of pupation the larvae were removed from the bark when the pupal chamber had been made and inserted in excavations made in cork, which were then covered with paper secured by pins. A day-to-day examination could then be made with the minimum of disturbance.

Preparations of whole mounts of the first and second stage larvae were made using acid fuchsin as the staining reagent according to the method described by Britten (1930). After boiling larval stages in caustic potash it was also found useful to examine them after clearing in cellosolve, thus avoiding the shrinkage and collapse of the exoskeleton.

For the permanent preparations of the gut, the whole of the alimentary canal was removed from the larva intact and preserved in Carnoy's fluid. The anterior hind gut was then embedded in 58° C. paraffin wax and the sections stained in Heidenhein's haematoxylin. The preservation and staining were, however, not regarded as completely satisfactory, and other methods will be used in a further investigation of the histological structure of the hind gut.

DESCRIPTION OF DEVELOPMENTAL STAGES.

The Egg.

The egg, which measures approximately 0·5 mm. × 0·3 mm., is normally lemon-shaped, with the micropyle occurring on a slight cone-shaped prominence (Plate I and fig. 15). Often the eggs are deformed as a result of being pressed into the cracks of the bark. The shell is sculptured with a honeycomb patterning and appears to be devoid of any adhesive coating. Its adherence to the bark is dependent upon the position in which it is deposited by the female.

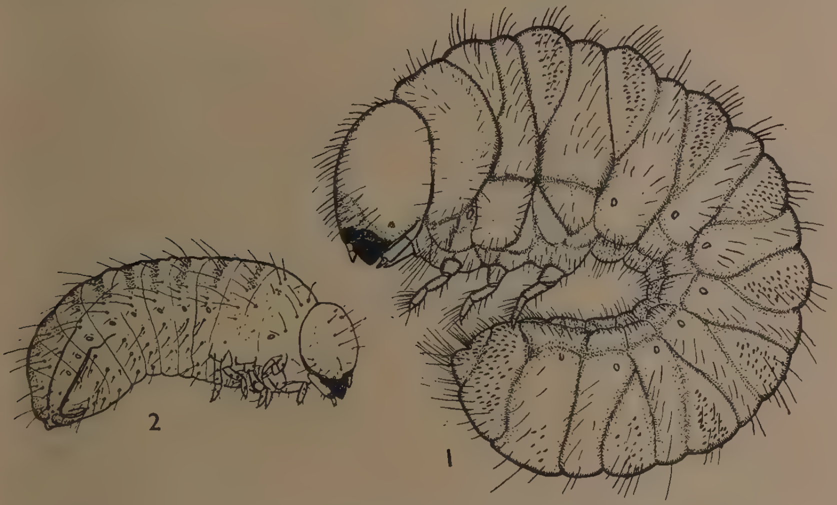
The Larva.

External Characters.

The scarabaeoid eruciform larva of *Ernobius mollis* (fig. 1) is typical of those of the wood-boring Anobiidae.

A detailed account of the full grown or nearly full grown larva is provided by Parkin (*l.c.*), together with figures of those features which distinguish it from other species.

The length of the full grown larva of *E. mollis* is given as 8 mm., and the setae are described as shorter and the prothorax less swollen than in the closely related *Xestobium rufovillosum.* The spinules on the prenotal folds occur on the metathorax and the first eight abdominal segments, laterally and dorsally on the ninth and laterally and ventrally on the tenth. The heavier chitinisation in the epistomal region in *E. mollis* occupies a rather larger area than in other species and is semicircular in outline.



Figs. 1, 2.—*Ernobius mollis* L. (1) Full grown larva. (2) First stage larva.

In a general description of the larva Perris (*l.c.*) allows only nine abdominal segments and thoracic legs of four segments. Parkin's account gives ten abdominal segments and five-segmented legs, with which my own observations agree. Both writers note the absence of ocelli, and on this point it should be mentioned that ocelli are, in fact, faintly discernible in many specimens.

The Early Stage Larva.

The early larva has not been described by any writer, but observations on the first stage larva of *Anobium punctatum* have been made by Gahan (1925) and on that of *Sitodrepa panicea* by Janisch (1923). Parkin (*l.c.*) also refers to the newly emerged larva of *Xestobium rufovillosum*. In all these species spinules are absent in the first stage and the larvae are straight-bodied and able to wander over the substratum.

As in the above species, the first stage larva of *Ernobius mollis* differs from the later stages in not adopting the scarabaeoid form (fig. 2), for the flexure of the body is a feature which develops gradually in the successive stages. The thoracic region is also comparatively less swollen in the earlier instars. The newly hatched larva measures 0·7 mm.–0·8 mm., and is immediately able to move freely over the bark. Progression is aided by the presence of two outpushings of the body wall in the form of conical cushions on either side of the anus (fig. 2, 3A). Janisch (*l.c.*) has noted similar structures, which he describes as prolegs, in the first stage larva of *Sitodrepa panicea*. If they can indeed be regarded as prolegs rather than highly modified anal cerci, the larva can be considered to hatch from the egg at an earlier ontogenetic stage than most coleopterous larvae. There are no setae or other ectodermal proliferations on the surface of these cushions, and they are no longer present in the second stage larva.

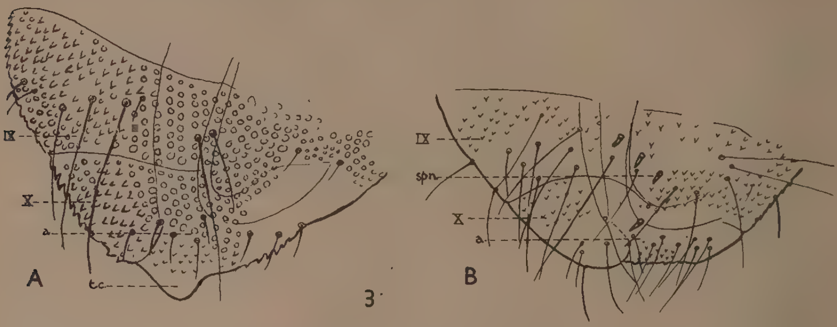


FIG. 3.—*Ernobius mollis* L. A. Terminal segments of abdomen of first stage larva B. The same of second stage larva. *a.*, anus; *t.c.*, terminal cushion; *spn.*, spinule; *IX*, *X*, ninth and tenth abdominal segments.

As in the other species mentioned spinules are absent in the first stage larva of *Ernobius mollis*, but they make their appearance after the first moult. The surface of the body wall of larvae at all stages is, however, not smooth; very small backwardly directed spines are developed from minute tubercles which occur all over the exoskeleton. The development of the spines is roughly prescribed in small band-like areas posterior to the region of the prenotal folds, although in the posterior region they are more generally distributed (fig. 2). Presumably the roughening of the surface of the body due to these small spines helps the first stage larvae to a certain extent in moving along within the bark much in the same way as do the spinules of later stages.

In the second stage larva spinules are present in a single row on the metathorax, on the first six, ninth and tenth abdominal segments. They are most numerous anteriorly, numbering twelve to fourteen on the dorsal and dorsolateral surface of the metathorax and first abdominal segment, and dwindle in number successively to the sixth abdominal segment, which carries two spinules only. Three or four spinules occur on each side of the ninth and one on each side of the tenth abdominal segments (fig. 3B).

In the third stage spinules occur in roughly double the numbers of the second stage, but they are still absent from the seventh and eighth abdominal segments.

The five segments of the thoracic legs are plainly visible in transparent preparations of the first stage larva (fig. 4). Eye spots are much more obvious in the newly hatched larvae than at any other time (fig. 15).

Digestive System (fig. 5A).

The length of the alimentary canal of a full grown larva is 15–16 mm.—almost three times that of the larva itself, the necessary folding of its length occurring in the abdominal region.

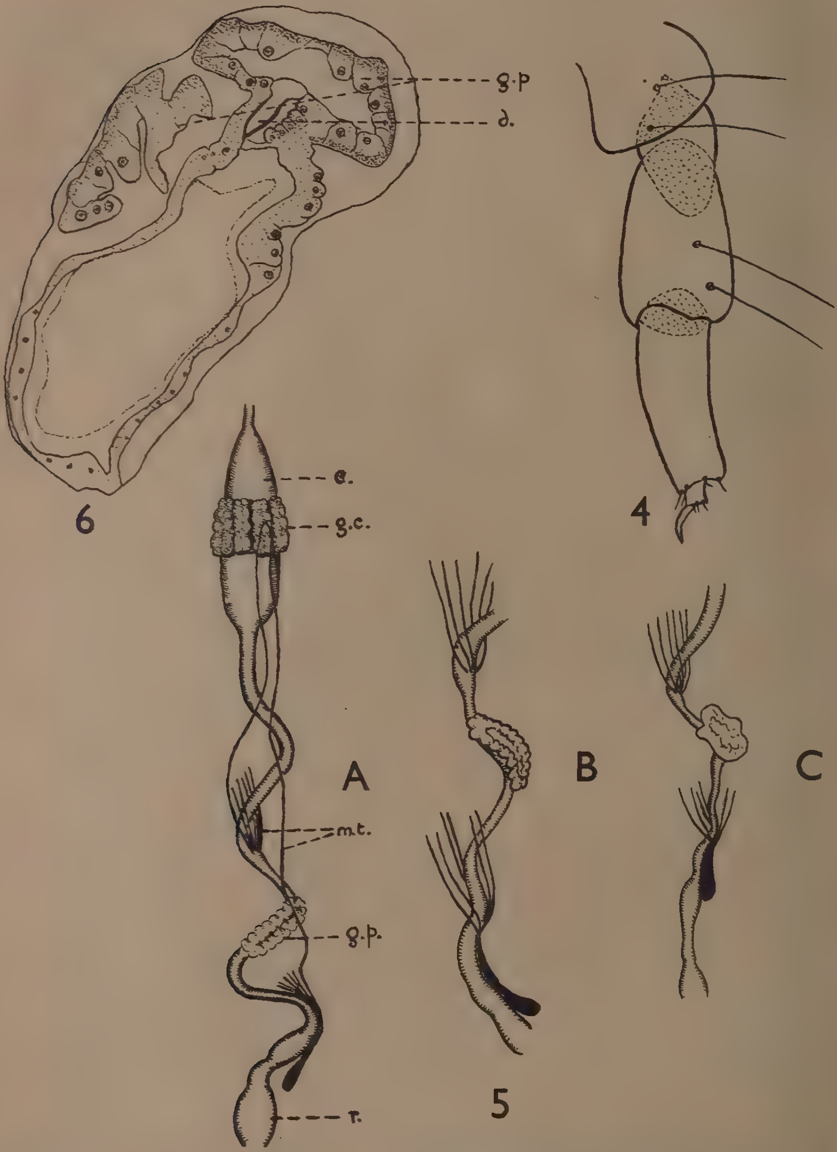
The stomodaeum consists of a narrow oesophagus, which on entering the thorax dilates almost immediately into the large thin-walled crop. This organ, in an active and feeding individual, is packed with chewed bark and almost completely fills the thoracic region.

On entering the abdominal region the gut narrows suddenly and gives rise to the gastric caeca. These organs are described by Breitsprecher (*l.c.*) and Müller (*l.c.*), who discuss their histology and microflora.

The caeca are four in number, two lying on either side of the mid-dorsal and mid-ventral line of the gut. They are about 1 mm. in length, and obscure the posterior part of the crop and anterior mid-gut since the space between the neighbouring caeca is extremely small. Antero-posteriorly each caecum is divided into two halves, each half consisting of a double row of four or five lobules of rather unequal size. The whole mass is of a uniform opaque white.

Posterior to the insertion of the gastric caeca the mesenteron widens to a diameter equal to the crop itself, and then gradually narrows as it proceeds on a straight course as far as the eighth abdominal segment. Here the intestine turns forward ventrally, and almost immediately the six malpighian tubules arise from its dorsal side, the length of the mid-gut being about 4–5 mm. One group of tubules passes to each side of the intestine, and winding forwards and backwards among its folds they terminate side by side on the rectal wall, invested by its peritoneal membrane, which holds them together. The blunt ending of this structure projects freely from the gut in the region of the seventh abdominal segment, about 2 mm. anterior to the anus.

The proctodaeum makes several convolutions in the region of the sixth and seventh segments. A thickening of the epithelium occurs on its ventral side in a position approximately one-third of the distance between the insertion of the malpighian tubules at the beginning of the proctodaeum and their termination on the rectum. This thickening forms a structure about 1 mm. in length running parallel with the length of the gut and embracing half its circumference. It is opaque white and its edges are slightly lobose. Kojima (1932) refers to a sac-like evagination of the gut in the region of the fore part of the hind intestine of the larva of the powder-post beetle, *Lyctus linearis*. Its position corresponds to that of the thickening described above in *Ernobius mollis*. Kojima gives no further description of this structure, however. In *Ernobius mollis* a preliminary histological investigation shows the thickening to be composed of much enlarged cells with correspondingly large well-staining nuclei (fig. 6). The cells are triangular in cross section, the cytoplasm of their



Figs. 4–6.—(4) *Ernobius mollis* L. One of thoracic legs of first stage larva. (5) A. Alimentary canal of larva of *E. mollis*. One of malpighian tubules drawn in entirety to show approximate course, remainder shown cut off at source and near termination. B. Hind intestine of *Xestobium rufovillosum* larva. C. Hind intestine of *Anobium punctatum* larva. *c.*, crop; *g.c.*, gastric caeca; *g.p.*, glandular pad; *m.t.*, malpighian tubules; *r.*, rectum. (6) *E. mollis*. Transverse section through hind intestine of larva, showing glandular pad. *d.*, duct; *g.p.*, glandular pad.

bases staining more darkly and being bounded by the peritoneal membrane. The inner narrow parts of the cells contain the nuclei in which the chromatin is arranged marginally; there is a centrally placed nucleolus.

What appears to be a central longitudinal duct occurs on the inner side of this pad of cells throughout its whole length. The position of the duct is clearly visible externally. The lining of the duct stains rather darkly, and it is probably a somewhat thickened region of the chitinous intima of the hind gut. Beneath this lining the epithelial cells are smaller than those which form the actual pad and their contours are more rounded. It is most likely that the duct opens into the hind gut lumen, although this opening has not at present been seen. Thus the organ would correspond with the " sac-like evagination " described for *Lyctus linearis*, the walls of the sac being formed from the much enlarged epithelial cells of the hind gut and its duct lining being continuous with the intima of the gut. It is possible that this structure is concerned with the reabsorption of water from the gut, and it would correspond with the rectal pads of other insects.

In *Xestobium rufovillosum* a similar organ is present in the same relative position (fig. 5B). It is well developed and of the same appearance as in *Ernobius mollis*. In *Anobium punctatum* (fig. 5C) it is present in the form of an apparently thin-walled pouch, little longer than broad and not nearly so obvious as in the other two species. Its position in the same relation to the insertion and termination of the malpighian tubules suggests that the structure is of the same nature.

From the seventh abdominal segment in which this pad occurs, the hind intestine runs forward to the fourth segment, passing insensibly into the rectum and from thence continues posteriorly straight to the anus.

The Pupa.

As in *Xestobium rufovillosum* (Fisher, *l.c.*), the exarate pupa of *Ernobius mollis* is mobile in the abdominal region and vigorous flexing movements are made when the insect is disturbed. Spinules are present on the metathorax and all visible abdominal tergites. These become less evident with the increasing age of the pupa, although they are present throughout the instar.

For the first two or three days the pupae are uniformly white. A pale brown pigmentation of the compound eyes and a darkening of the edges of the mandibles are the first colorations to appear. Gradually during the next six days or so the pigmentation of the eyes deepens to black and the wings may be observed to be turning grey. There follows a gradual pigmentation of all the appendages, including the genital appendages of the posterior segments of the abdomen, and this is succeeded by a general coloration of the whole body. The beetles which emerge from the pupal skin are pale in colour and darken to the characteristic reddish brown with increasing age.

The unspecialised segments of the abdomen are visible as terga 1 to 8 and sterna 2 to 8.

Metcalfe (1932) has given an account of the development and appearance of the genital appendages in the pupae of *Sitodrepa panicea* and a description of the condition in the pupae of *Xestobium rufovillosum* is given by Fisher (*l.c.*).

The female appendages of *Ernobius mollis* do not differ greatly from those of the above two species (fig. 7A, 7B).

In the early female pupa the posterior margin of the eighth sternite is somewhat tumid, with a posterior central indentation and single row of setae upon the crest of the tumid border. The gonopore is borne on the ninth sternal plate and is faintly discernible as a small depression. The plate is divided into two raised processes on either side of the gonopore, each process carrying a palp. These two palps, which are the precursors of the mesocerci of the imago, are two-segmented, the proximal segment being large and rounded and the distal segment being small, tapering and turned outwards. Dorsal to these appendages two plates are visible, folded one over the other beneath the eighth tergum. The more dorsal of these has an entire margin, while the more ventral plate is trilobed, the central lobe being emarginate; the site of the future anus appears to lie between them.

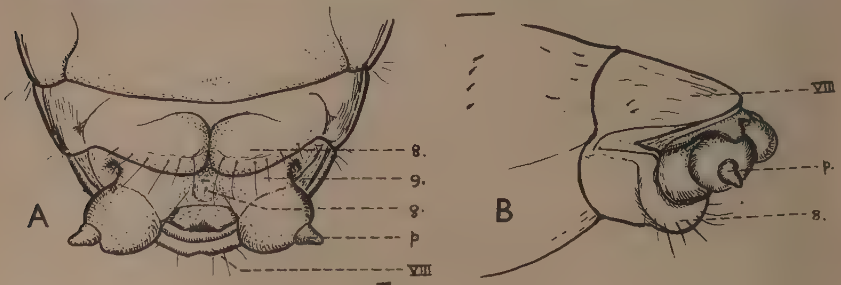


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Fig. 7.—*Ernobius mollis* L. A. Ventral view of posterior segments of female pupa. B. Left lateral view of same. *g.*, gonopore; *p.*, distal segment of palp; *VIII*, eighth abdominal tergite; *8*, *9*, eighth and ninth abdominal sternites.

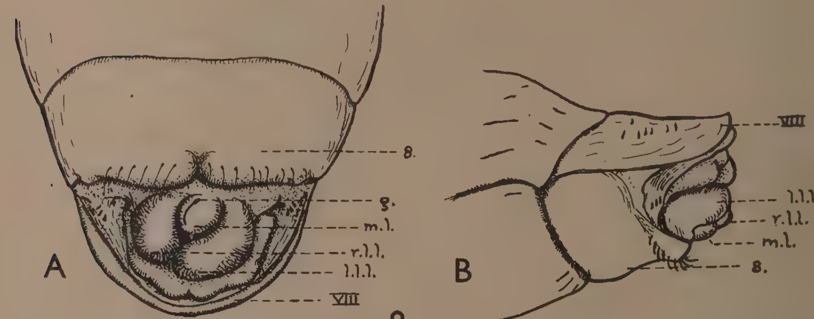

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Fig. 8.—*Ernobius mollis* L. A. Ventral view of posterior segments of abdomen of male pupa. B. Left lateral view of same. *g.*, gonopore; *l.l.l.*, left lateral lobe; *m.l.*, median lobe; *r.l.l.*, right lateral lobe; *VIII*, eighth abdominal tergite; *8*, eighth abdominal sternite.

In older pupae in which chitinisation beneath the pupal skin is plainly visible, the ninth sternite is seen to have elongated and the gonopore moved slightly posteriorly. Chitinisation of the sternum occurs on either side of the mid-line in two plates, the fusion of which gives rise to the ovipositor. The chitinous segments of the mesocerci are visible within the original pupal structures, the proximal segment being now narrow and parallel-sided as in the imago. The mesocerci stand thus on the ventro-lateral posterior margin of the developing ovipositor with the gonopore between them.

In the male pupa (fig. 8A, 8B) the eighth sternal plate is not so tumid as in the female and the posterior margin is not so strongly indented. The ninth sternum carries three prominent appendages, two of which are crescent-shaped and represent the right and left lateral lobes of the anlage of the aedeagus. Together they embrace the median lobe, which is circular in outline and carries the gonopore. These appendages are somewhat asymmetrical, the left lateral lobe being larger than the right lateral lobe and the gonopore being situated on the posterior right side of the median lobe. The arrangement of the plates dorsal to the genital appendages is similar to that in the female. In some specimens a small group of spinules is to be seen on the ventral borders of the apparent ninth tergum, presumably the relics of the lateral spinules of the ninth abdominal segment of the larva.

In the general arrangement of the structures mentioned the male pupa of *Ernobius mollis* appears to be similar to that given for *Sitodrepa panicea* (Metcalf, *l.c.*), though the relative sizes of the right and left lateral lobes are reversed in the two species.

The Imago.

External Characters.

Detailed descriptions of the external features of the imago have been given by Perris (1854) and by Tooke (1945).

There is a considerable variability in the size of the beetles, the range for the females being wider than that for the males. The average length of the female is also significantly greater than that of the male; thus the average length of the female measured when at rest (i.e., excluding the head) is 4·5 mm. with a range of from 3·2 mm. to 6·0 mm., while the corresponding figures for the male are 4·1 mm., 2·9 mm. and 5·4 mm. respectively.

The compound eyes are large in both sexes, but are especially large and prominent in the male.

More positive sexual differences are to be seen in the antennae and the termination of the abdomen.

In the male the antennal club of three segments exceeds the total length of the proximal segments. Thus, when at rest beneath the body, the proximal segments extend as far as the coxae of the meso-thoracic legs and the club as far as the middle of the abdomen. In the female the proximal segments also reach to the second coxae, but the club does not extend beyond the thorax. In addition, the antennae of the male are more slender than those of the female and the segments of the club have parallel sides. In the female the segments of the club broaden distally and their sides are somewhat curved, though there is a certain amount of variability in the curvature and they sometimes approach the straight-sided form of the male.

The last externally visible tergum of the abdomen in the male is convex laterally, somewhat concave antero-posteriorly so that the posterior edge turns up slightly. In the female the last visible abdominal segment is convex dorsally both laterally and antero-posteriorly so that the posterior edge is slightly turned downwards. This is quite constant, and is a reliable character for distinguishing the sexes, the other external sexual differences being subject to slight variation.

Digestive System.

The alimentary canal of the imago is approximately 10 mm. long ; it is thus considerably shorter than that of the larva.

The narrow oesophagus dilates into a large thin-walled crop on entering the abdomen. This part of the alimentary canal is usually distended with air, as it and the succeeding parts of the digestive tube as far as the rectum are devoid of any food contents.

The crop narrows to pass into the proventriculus, which, at its junction with the mid-gut bears, as in the larva, four lobulated gastric caeca. These are, however, relatively smaller than those of the larva.

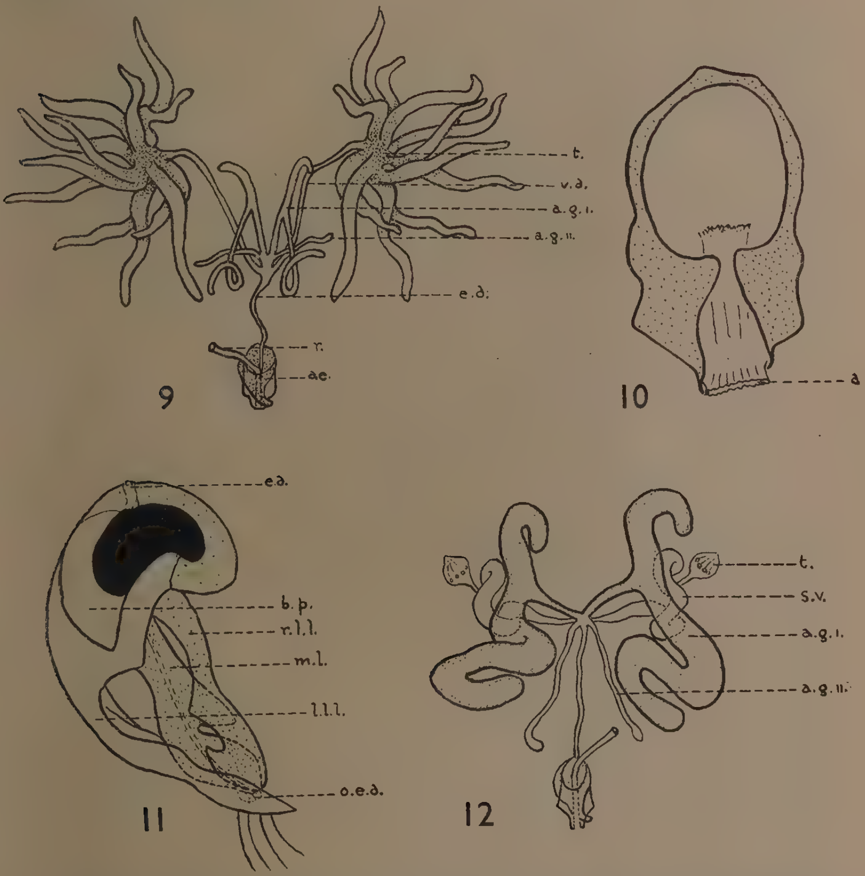
The succeeding part of the intestine is folded upon itself rather to the left side of the insect, dorsal to the reproductive organs. The mid-gut is short, being about 1·5 mm. in length, and the six malpighian tubes arise at its junction with the hind-gut in the same manner as in the larva. The fold of the hind intestine passes forward and then passes back as the rectum, slightly on the right and dorsal to the reproductive organs of that side. The pad of glandular tissue noted in the hind gut of the larva is absent as such in the imago, but the thickened region is intimately attached to the hinder part of the rectum, so that a loop is formed in that part of the gut which lies between the insertion of the malpighian tubules and posterior to their termination on the rectal wall. The purpose of this arrangement is not clear, but it may be related to the reabsorption of water from the gut. The termination of the malpighian tubules is similar to that in the larva in that the blind ends lie parallel to the rectum and are invested in its peritoneal membrane. However, they do not project from the gut wall at their termination as in the larva, but remain closely applied to the side of the rectum.

The rectum is recognised by its dark brown faecal contents, which are probably the remains of the last larval meal.

The rectum terminates at the anus at the posterior border of the ninth sternite in the male and anterior and dorsal to the gonopore in the ovipositor of the female.

Male Reproductive System.

The appearance of the male reproductive organs varies with the age of the imago. Prior to emergence from the wood the testes are the predominant organs, and are seen as paired structures occupying the greater part of the abdominal cavity (fig. 9). Each testis consists of twelve follicles, which are finger-shaped and tapering distally. The vasa deferentia into which the follicles open are at this stage narrow, almost straight tubes which run diagonally towards the middle line, where they unite to form the ejaculatory duct. At the point of junction of the two vasa deferentia opens the common duct of the two paired accessory glands. The more anterior pair is the larger, each member consisting of two limbs running antero-posteriorly. The forward limb is the shorter and bends distally in a hook shape, while the other limb, which is nearly twice as long, passes posteriorly and then loops over itself in a lateral direction. The short ducts from these glands meet in the mid line, and at the point of their union the openings from the second pair of accessory glands are received. In the early stages these are short, straight, narrow glands running out laterally from the mid line, ventral to the posterior limbs of the anterior pair of glands, and joining the duct from the latter on its dorsal side. The very short common duct from the accessory glands joins the vasa deferentia anteriorly as the latter unite to form the ductus ejaculatoris. Thereafter the ductus ejaculatoris proceeds as a straight and narrow tube until it enters the aedeagus. The genital armature is covered by the ninth sternite (fig. 10). This is in the form of a chitinous ring anteriorly and expands into two emarginate plates posteriorly. The rectum traverses its length, and the expanded plates embrace it as it passes through to open on the anus on the posterior border.



FIGS. 9–12.—*Ernobius mollis* L. (9) Immature male reproductive system dissected from the dorsal side. *ae.*, aedeagus ; *a.g.I.*, *a.g.II*, anterior and posterior accessory glands ; *e.d.*, ejaculatory duct ; *r.*, rectum ; *t.*, testis ; *v.d.*, vas deferens. (10) Ninth sternite of male. *a.*, anus. (11) Dorsal view of genital armature of male. *b.p.*, basal piece ; *e.d.*, ejaculatory duct ; *l.l.l.*, left lateral lobe of aedeagus ; *m.l.*, median lobe ; *o.e.d.*, opening of ejaculatory duct ; *r.l.l.*, right lateral lobe of aedeagus. (12) Mature male reproductive system dissected from dorsal side. *s.v.*, seminal vesicle.

The form of the aedeagus has been described by Sharp and Muir (1912) in a comparative account of the male genital tube in Coleoptera.

The whole of the structure lies slightly on its side with the dorsal surface turned towards the right (fig. 11). Thus the genital opening is ventral to and to the right of the anus.

The tegmen or basal piece and the bases of the right and left lateral lobes form a bulb which envelopes the base of the median lobe. Both lateral lobes and median lobe are asymmetrical, the median lobe being tubular proximally and flattened at the apex. The ejaculatory duct enters the genital pocket dorsally and traverses the median lobe to open on its blunt apex.

As the beetles become mature the sperms leave the testes and accumulate in the vasa deferentia, which develop into the enlarged and conspicuous seminal vesicles (fig. 12). In the fully mature beetle prior to copulation these distended seminal vesicles are now somewhat twisted upon themselves and their contents give them a creamy-white glistening appearance, while the testicular follicles have disappeared and the remains of the testes have become inconspicuous bodies, pointed anteriorly and wider where they are attached to the vasa deferentia. Anteriorly a small portion of the vas deferens remains narrow and free from spermatozoa. Concurrently with these changes, the anterior accessory glands enlarge enormously, becoming much twisted upon themselves and so filled with a white secretion as to be quite turgid. The second pair of glands also elongate considerably, and the diameter of the glands is correspondingly increased although they remain almost transparent.

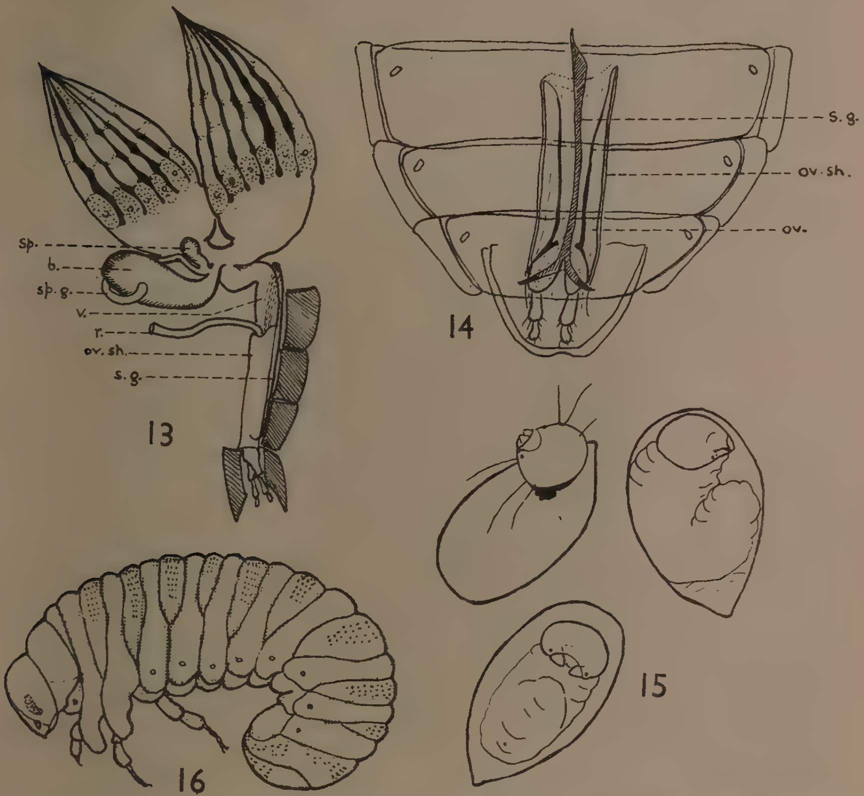
Female Reproductive System.

The paired ovaries are composed each of twelve ovarioles of the acrotrophic type (fig. 13). These ovarioles are arranged in each ovary in two rows of six and open thus into the dilated egg calyx of the ovary. The median ligament formed from the united terminal filaments is attached far forward in the thoracic cavity in the region of the crop.

The two short oviducts pass inwards and somewhat posteriorly to unite in the vagina and at this point the bursa copulatrix and spermatheca occur as dorsal evaginations of the genital tube. The bursa is a relatively large pear-shaped structure attached to the vagina by a narrow neck, and passing forwards to lie between the bases of the ovaries and dorsal to them and the oviducts.

The spermatheca, which is also pear-shaped and about one-quarter the size of the bursa, opens into the latter at the base of the neck region. At this junction arises the spermathecal gland which is tubular in form and of a length considerably in excess of that of the bursa. It partly encircles the latter, passing forwards ventrally to it and curving over to run posteriorly and end blindly on the dorsal side of the bursa.

The vagina, which is of fairly uniform width throughout its length, is folded forward upon itself before passing back to enter the ovipositor, thus allowing for extension during the process of egg-laying. The vagina is joined by the rectum as it enters the ovipositor, and the two traverse the length of the ovipositor together, the rectum dorsal to the vagina. The ovipositor itself is typical of those occurring in the Anobiidae and has been described in detail by Breitsprecher (*l.c.*), together with those of several other species of the Anobiidae. It is a chitinous cylinder which occupies when at rest almost the whole length of the last four segments of the abdomen (fig. 14). The suggested homologies of the coleopteran ovipositors and associated structures are reviewed and their development discussed by Metcalfe (1932), with special reference to the conditions in *Sitodrepa panicea*. In common with other species, the gonopore in *Ernobius mollis* is bordered by chitinous plates which probably represent the ninth sternite, and which bear a pair of two-segmented setaceous palps on their margins. This arrangement differs from that of *Sitodrepa panicea* in which there is a single asymmetrical palp and agrees with that for *Xestobium rufovillosum* (Fisher, *l.c.*) and *Anobium punctatum* (Breistprecher, *l.c.*). The ovipositor is invested by a membrane, the ovipositor sheath, which represents the intersegmental membrane between the terminal external abdominal segment and the penultimate segment contributing in the formation of the ovipositor. In many of the Anobiids, intersegmental glands occur as tubular evaginations of this membrane in the region of its connection with the proximal end of the



FIGS. 13–16.—*Ernobius mollis* L. (13) Immature reproductive system of female seen from right side. *b.*, bursa copulatrix ; *ov. sh.*, ovipositor sheath ; *r.*, rectum ; *s.g.*, spiculum gastrale ; *sp.*, spermatheca ; *sp.g.*, spermathecal gland ; *v.*, vagina. (14) Dorsal view of terminal abdominal segments of female showing ovipositor in transparency. *ov.*, ovipositor ; *ov. sh.*, ovipositor sheath ; *s.g.*, spiculum gastrale. (15) Eggs with larvae hatching. (16) Prothetelic larva.

ovipositor (Breitsprecher, Metcalfe, Fisher, *l.c.*), but these are entirely absent in *Ernobius mollis*. The function of these glands in relation to the transference of the symbiotic yeasts they contain has been described by Breitsprecher. In *Ernobius mollis*, glands of similar function have been demonstrated by the same author in the wall of the vagina itself, while the yeasts are located in the cavity of the vagina in the region of the glands and are sheltered in this position under chitinous hairs.

The spiculum gastrale is a chitinous rod representing the modified seventh sternite (Breitsprecher). It is of the same length as the ovipositor, in relation to which it lies ventrally; the two structures are attached at their proximal ends by muscles, and the spiculum affords a basis for the retraction of the ovipositor when it is withdrawn into the abdomen. At the distal end the chitinous rod bifurcates and the short, splayed-out arms turn slightly dorsalwards, forming a kind of cradle for the terminal part of the ovipositor when it is at rest.

Fig. 13 shows the appearance of the reproductive organs of the immature female beetle prior to its emergence from the bark.

Mature females differ only in the condition of the ovarioles, which become distended with eggs, and in the mated female, in the relatively greater size of the bursa copulatrix, which is now distended with sperm.

BIOLOGICAL STUDIES.

Habits of the Imago.

Kemner (1915), working in Sweden, states that the beetles swarm during the summer, emergence taking place fairly continuously throughout that season and that pairing occurs in May and August. According to this writer, the eggs which are laid in the earliest swarming give rise to an autumn generation of beetles.

Tooke (1945), referring to the conditions in South Africa, says that the beetles begin to emerge in August and September out of doors and so continue during the whole summer, and that indoors, in heated rooms, they may be found throughout the year.

In this country, the main emergence period outdoors and indoors is late June, July and early August, pairing being continual throughout these months. Under room conditions the most advanced beetles may be expected to be seen at the end of May, 26th May being the earliest in my records. Stragglers continue to emerge throughout September and even exceptionally in October. Three such late beetles, all female, which were observed on one occasion to emerge in the first week in October existed in a quiescent state during the following very mild winter. It is possible that the beetles are capable of enduring the winter and breeding in the following spring, although these particular specimens lived only until February or March.

In this country there is only one generation of beetles during a single season; on no occasion has there been evidence that the life-history can be completed in less than about one year. It is true that bark infected with *Ernobius mollis* generally contains larvae in a complete gradation of size, and although samples taken in spring and in late summer contain at the same time very small and very large larvae, suggesting the presence of two generations, as will be shown later, this discrepancy in size is due to an inequality in the growth rate of the larvae, some of which require more than a year to complete their development.

The beetles emerge from the bark by flight holes of diameter 2 mm. or thereabouts. In making their exit they will bore through materials other than bark such as wood, paper or cloth, should these obstruct their passage.

During the day the beetles which have emerged tend to hide away from the light, although in hot weather they are much more active and pairing will take place in day-time as well as at night.

Both sexes have fully developed reproductive organs when they emerge from the bark and they are capable of pairing at once. The organs become fully mature during the period that the beetle remains within the bark after the pupal ecdysis—a period of about six to twelve days. It is clear, however, that the reproductive organs are functional a few days before the beetles emerge, for on many occasions these resting beetles have been removed from the bark to pair up for breeding purposes and copulation has taken place without delay. On the other hand, beetles removed from the bark soon after they have emerged from the pupal skin have not paired for about ten days. Reproductive organs dissected out from imagines in which the exoskeleton had not reached full pigmentation showed in the male large testicular follicles, accessory glands incompletely developed and empty seminal vesicles, and in the female, ovarioles with even the most advanced ova in an immature condition.

Normally the beetles pair within a few hours of emergence from the bark, but under unfavourable conditions pairing may be delayed and has been observed to take place as long as twelve days after emergence.

A firm connection between the individuals is maintained in an end-to-end position, the sixth abdominal segment of the female entering entirely into that of the male (Sharp, 1916).

The beetles generally remain in copula for about twenty-four hours, during which time they often hide in crevices of the bark or in old flight holes. They may remain paired for much longer, however, periods of three days being quite frequent, and even as long as six days is not uncommon. Lengthier periods than this are possibly due to some maladjustment of the coupling mechanism and generally results in the death of the beetles.

Repeated pairing between the same beetles sometimes takes place, the female laying eggs between successive copulations.

Oviposition.

Oviposition usually begins very soon after the copulants have separated. In most cases the female is laying in one or two days' time, but in certain circumstances this may be delayed for several days. Such delay occurs if the bark provided for egg-laying is not of a type favoured by the particular individual. Delays of up to six days have been observed and in some cases no laying has occurred at all. In this connection it is of interest to note that females themselves bred in spruce bark could not be induced to lay their eggs on larch, although the transplanted larvae could work in larch bark quite satisfactorily.

Ernobius mollis is always more active at night and it is fairly certain that oviposition takes place only in the hours of darkness ; it has never been observed by me in prolonged examinations of the beetles during day-time throughout the breeding seasons of several years, whereas on many occasions it has been watched taking place at night. The artificial light used for the purpose of this observation does not seem to act as a deterrent and the female appears to be completely indifferent to it. Before ovipositing, the female runs over the bark, exploring the surface with her antennae. On reaching a suitable site she stops and the ovipositor makes its appearance, the terminal palps seeking out crevices. The ovipositor is then fully extended and thrust into the crevice; about thirty seconds later it can be seen to be distended by the egg as the latter makes its way to the exterior.

The egg advances down the ovipositor with the micropylar end hindmost so that when the egg is laid in a vertical position the micropyle is uppermost. Frequently, however, they are laid so that they lie on their sides. Generally a small number of eggs is laid in a group, the numbers depending on the suitability of the site. Favoured positions are round the base of twigs and under flakes of bark, in which position the eggs are often strongly depressed and misshapen. Such deformed eggs appear to hatch normally as a rule. In the laboratory the sawn ends of wood and bark are favourite sites, as the numerous indentations hold the eggs firmly. As the larvae are easily able to wander over the surface there is no advantage in the female restricting her oviposition to the bark.

Kemner (*l.c.*) gives the number of eggs laid by a single female as ten to fifteen. The numbers do, in fact, vary very greatly, at all events under laboratory conditions. Frequently they do not exceed or are less than Kemner's figures, but more often greater numbers are laid, as is shown in Table I. Observations during the summers of 1947 and 1948 gave average numbers of eggs laid per female under laboratory conditions as fifteen and twenty-six respectively. The maximum number of eggs observed to have been laid by any single female is sixty-six and no doubt this number may sometimes be exceeded. Dissected specimens have shown each ovariole to be capable of producing at least five eggs, so that the egg-laying potential of the beetle should be of the order of 120.

TABLE I.

Duration of egg-laying period (days).	Number of eggs laid.	Duration of egg-laying period (days).	Number of eggs laid.
9	35	1	2
3	3	5	31
1	1	5	27
7	11	2	22
8	35	1	24
5	10	2	16
2	8	2	25
1	3	1	8
4	19	7	24
2	5	6	20
5	30	5	19
2	14	5	20
2	10	5	23
1	2	1	25

Table I shows also the duration of the egg-laying period of individual females. It will be seen that here again there is great variability in the behaviour of different individuals. Nine days was the most extended period recorded, during which time thirty-five eggs were laid. On the other hand, several individuals laid on one night only, the number of eggs laid in each case varying between one and twenty-five. Janisch (1923) found a similar irregularity in *Sitodrepa panicea* with an egg-laying period varying from one to twenty days and the number of eggs laid per day from one to twenty-seven.

After pairing, the male, and after oviposition, the female, become quiescent and remain so until they die, both sexes living for any period up to about one month after emergence. Neither sex has ever been observed to feed at any time after emergence. Dissections always show a gut completely empty with the exception of the hind gut, which contains a dark brown material which is probably the remains of the last larval meal. This corresponds with the condition found by Fisher (1937) for *Xestobium rufovillosum.*

Duration of Egg Period.

The incubation period of the eggs of *Ernobius mollis* is, under laboratory conditions, about ten days to three weeks with an average of thirteen to fourteen days. No doubt the temperature and other external factors influence the rate of development to some extent, as was found by Janisch for *Sitodrepa panicea* ; however, the normal variations in temperature encountered in different summer seasons seem to have little effect, no significant difference being observed in the average incubation period in successive years.

Larval Studies.

Hatching and Penetration of the Bark.

Just prior to hatching the eggs become more opaque. Apparently the larva can move freely within the shell and consequently can hatch from either end of the egg (fig. 15). In hatching, the larva eats part of the shell and commonly feeds upon the remains after it has emerged.

The viability of the eggs is extremely high, a hatching rate of not less than 84 per cent. being obtained in the laboratory.

The first stage larva is able to move fairly rapidly over the bark and may wander for one or more days, covering a distance of several centimetres. The protuberances on either side of the anus probably function in much the same way as do the terminal cushions of a polypod larva and give impetus from behind.

Boring may be begun very soon after hatching, but often the first attempts to penetrate the bark are abortive and larvae are still found wandering over the surface a day or two after hatching. Common sites of penetration are round knots and in the sawn edges of bark.

Once the larva has entered the bark it adopts the flexed posture characteristic of the group, with the head and posterior end of the abdomen presented to the entrance. Entry holes are detected by small piles of transparent faecal pellets of the same colour as the bark. In this superficial position in the bark, the first stage larva makes a number of blind galleries radiating from the point of entry, about 1 mm. below the surface and $\frac{1}{4}$ to $\frac{1}{2}$ mm. wide.

Growth and Moulting of the Larva ; Diapause.

Since the larva of *E. mollis* is restricted to the bark it is comparatively easily found and observed. For several reasons, however, its growing period is not so easily studied as might be expected, and the duration of the first stage is the only point on which information can be given with any confidence.

The usual method of determining the number of instars by the recovery of the cast skins cannot be used because the larvae very frequently eat them almost as soon as they are shed. This difficulty became apparent early in the investigation, and it was therefore decided to undertake the measurement of the head size of a large number of individuals, as it was thought possible that the measurements might fall into sufficiently well-defined groups to correspond with the successive instars. This method was used by Metcalfe (1932) in an attempt to estimate the number of instars during the development of *Sitodrepa panicea* and in order to determine if Dyar's law could be applied to the species.

Although Metcalfe was able to reach certain conclusions as a result of her investigations, she found the method unsatisfactory for determining the number of the instars partly because of the periodicity of the egg-laying in *Sitodrepa panicea*, which gave an insufficiency of young larvae in her samples. This particular difficulty did not apply to *Ernobius mollis*, as larvae of all ages were available. Metcalfe also found her data complicated by the variation in size in the larvae of any particular stage which gave a presumed overlapping in the size of the instars. Until the investigation had been made it was, of course, impossible to tell whether this difficulty applied equally to *Ernobius mollis*. By measuring larvae of known age it was thought that if the number of instars could be demonstrated by this method, a rough indication might be obtained of the duration of the successive stages.

Accordingly, larvae of known age were removed from the bark and measured, the head length from vertex to tip of mandible being used as a criterion.

Some 150 larvae were measured in this way, but the scatter in the measurements obtained was far too great for any size grouping to emerge from them. There was a continuous gradation of head length between 0·10 mm. and 1·3 mm. Also, after the first instar, the variability in these measurements increased as the larvae grew older and ceased to bear much relation to their age.

The reason for this was explained by observations on larvae which had hatched during the previous summer. Towards the end of the season many of these metamorphosed, completing their life-history in one year. Others did not and were requiring two years or possibly more for their development. Thus, samples of larvae of any one age included some of each of these categories, with a consequent variability in their size.

An attempt to determine the number of instars by repeated measurements of individual larvae, all of which hatched in September, met with little success. Larvae do not survive well if repeatedly disturbed and the mortality was too heavy to reach any conclusions relating to the number of moults. It was found, however, that at any rate for larvae hatched late in the season, the first stage lasts approximately one month.

Most of the larvae which survived repeated measurement passed into a state of diapause in their second or third stage, in which condition they remained throughout the winter.

Winter measurements of larvae show that, as might be expected, those which hatch early in the previous summer attain a larger size than those hatching late.

Table II shows the mid-winter measurements of the head length of twenty-three larvae hatched in late June or early July of 1947 and those of forty-four larvae hatched during August of the same year. There is a significant difference between the mean value of 0·82 mm. for the early hatched larvae and 0·40 for the late hatched larvae.

Table III shows figures for the head measurement of twenty-one first stage larvae and those for twenty-two in the second stage. The mean values for these are respectively 0·17 mm. and 0·27 mm. No mean value has been obtained for the full grown larva owing to the difficulty of knowing beforehand when the last stage has been reached, but the head measurement of the largest larvae measured has never exceeded 1·30 mm.

TABLE II.

	June–July hatching. Head length (mm.).	August hatching. Head length (mm.).	
	1·30	0·90	0·35
	1·20	0·90	0·35
	1·20	0·80	0·35
	1·15	0·70	0·35
	1·10	0·60	0·35
	1·10	0·55	0·35
	1·05	0·50	0·30
	1·00	0·50	0·30
	1·00	0·50	0·30
	0·95	0·50	0·30
	0·90	0·45	0·30
	0·85	0·45	0·30
	0·80	0·45	0·30
	0·70	0·40	0·30
	0·70	0·40	0·30
	0·65	0·40	0·25
	0·60	0·40	0·25
	0·55	0·40	0·25
	0·50	0·40	0·25
	0·50	0·40	0·20
	0·45	0·40	0·20
	0·30	0·40	
	0·30	0·40	
Mean value .	0·82	Mean value . 0·40	

TABLE III.

	First stage larvae. Head length (mm.).		Second stage larvae. Head length (mm.).	
	0·20	0·15	0·40	0·25
	0·20	0·15	0·35	0·25
	0·20	0·15	0·30	0·25
	0·20	0·15	0·30	0·25
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Mean value .	0·17		Mean value . 0·27	

It will be seen from a comparison of the individual figures in the tables that a high proportion of the larvae hatched late in the season must overwinter in their second stage, whereas many of the early hatched larvae overwinter in the late stages. It is significant that small larvae are rarely found working in the bark in the winter-time, whereas the large-sized larvae are found feeding and actively tunnelling more often than not.

The above points suggest that the development of the larvae hatched late in the season is retarded by the onset of diapause, which, it appears, supervenes in the second or the third stage.

The larvae in diapause are probably the individuals which take more than a year for their development. If this is the case, over-wintering larvae with large head measurements should give a greater proportion of imagines in the following summer than those with small head measurements. Observations on these lines suggest that this is the case, but available material was not sufficient to draw any definite conclusions.

The time at which the egg is laid, therefore, is probably an important factor in determining the length of the development period. Doubtless other factors are responsible as well. Kelsey (1946) mentions "adverse conditions" causing the larvae to remain in the wood for two or more years. If the presence or absence of diapause influences the rate of development, then this rate will depend on the presence or absence of factors inducing a diapause. Diapause has been inadvertently induced in *E. mollis* at various stages. Introduction of the larvae into a new piece of bark, for example, will often bring this about. Prothetely, which may be regarded as a special case of diapause, has been noted on two occasions (Gardiner, 1951), and was apparently induced on the one hand by starvation and on the other by physical damage to the insect at a critical stage. Clearly *E. mollis* is one of those insects in which there is a latent tendency towards diapause (Wigglesworth, 1939) and, as the cockchafer *Melolontha*, it appears to be able to hibernate in various stages and exceptionally as an adult (see p. 16).

The fact that young larvae are nearly always to be found in a state of inactivity during the winter points to a seasonal diapause common to many species of insects. As has been pointed out by Simmonds (1948) every insect has a set of conditions favourable to its development at a certain stage, and the conditions common in the fall of the year are probably more unfavourable to the young larvae of *Ernobius mollis* than to the later larval stages. The fact that the larvae are not always found in a state of inactivity would be explained by Simmond's contention that there would be among individuals a variable susceptibility to enter a state of diapause, for the genetical constitution of the insect governs its reactions to its environment. The fact that *Ernobius mollis* larvae of the same brood but of completely different sizes may be found side by side with only the wall of the gallery between them could, in fact, be explained only on a genetical basis.

Pupation.

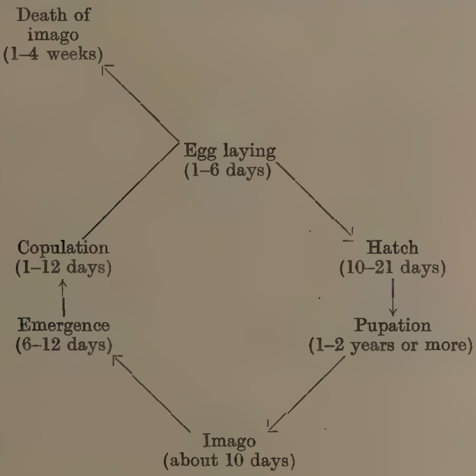
Pupation takes place under laboratory conditions from May to September. An oblong cell is constructed at the end of the final gallery in the bark, lying parallel with the surface and generally penetrating the outer part of the wood. The communication with the gallery is blocked by the larva with a cementing mass of faecal pellets and chewed wood. A few days after its construction the onset of pupation is observed. The larva stretches out, and first the head and then the thoracic appendages lose mobility. The pre-pupal phase follows, the rudiments of both pairs of wings being clearly visible as latero-ventral swellings in the thorax and the abdomen tapering posteriorly.

The prepupal phase lasts for one or two days before the final larval ecdysis.

The pupal stage lasts for ten days or rather less. Prior to metamorphosis, the appendages can be seen pulsating within the pupal skin. The newly emerged beetle is almost colourless in the body parts. The appendages are yellow and the edges of mandibles are deeply pigmented. There is also pigmentation along the edges of the abdomen. A further six to twelve days are spent in the bark by the young imago before it finally emerges, and during this period the colour darkens and the reproductive organs become mature.

Summary of Life Cycle.

The life cycle of *Ernobius mollis* is summarized in diagrammatic form below, the figures indicating the period between the named and the previous stages.



SUMMARY.

The present distribution of *Ernobius mollis* is given, together with a list of the species of trees in which infestation of the bark by *E. mollis* has been recorded.

The external characters of all stages of the insect are described, in the larva with special reference to the early stages which have not previously received attention, and in the pupa with detail of the developing genital appendages. The alimentary canal of larva and imago and reproductive organs of the male and female beetle are described.

A sequence of the life history and habits of the insect is included, with special reference to the moulting and growth of the larvae.

ACKNOWLEDGMENTS.

I wish to express my thanks to Dr. R. C. Fisher of the Forest Products Research Laboratory for his invaluable guidance in the preparation of this work, and to Dr. D. R. Crofts of Queen Elizabeth College for her advice and encouragement.

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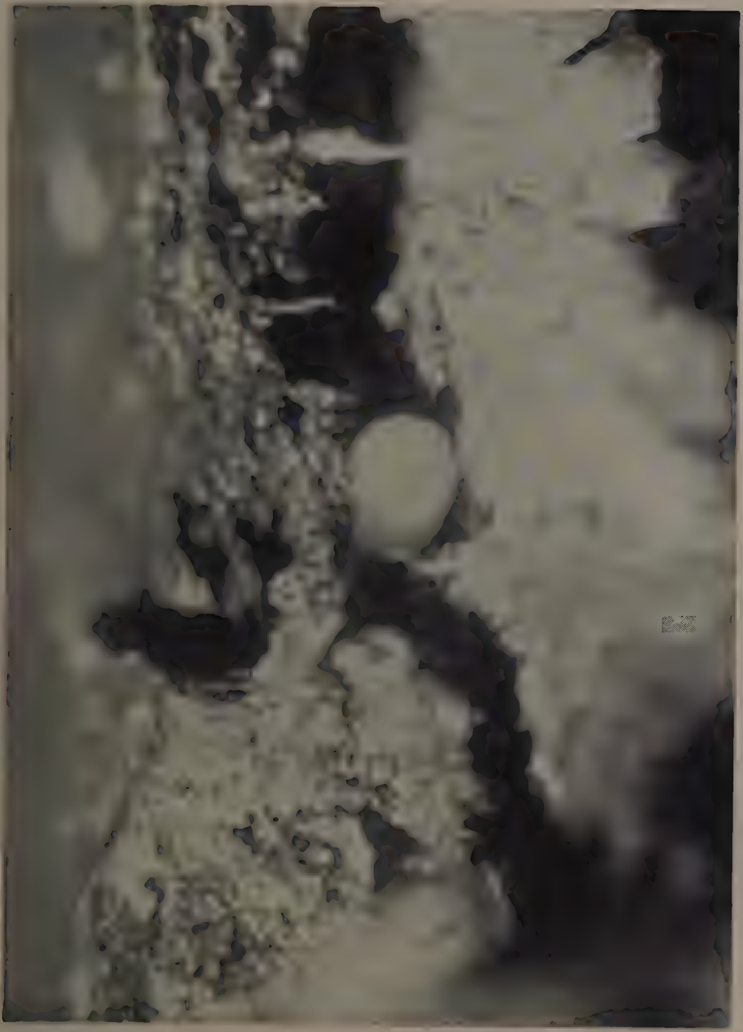

PLATE 1.—EGG OF *E. mollis* IN CREVICE OF BARK.

Miss Phyllis Gardiner.

Adlard & Son, Ltd., Dorking.

Vol. 104. Part 2. Pp. 25–37, 5 figs. 15th April, 1953

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ON THE EXTERNAL MORPHOLOGY OF THE NECK AND THORAX IN *FORFICULA AURICULARIA* L. (DERMAPTERA).

By H. Henson, D.Sc., Ph.D., F.R.E.S.
(*Lecturer in Zoology, University of Leeds*).

Manuscript received 18th June, 1952.
(Read 3rd December, 1952.)
With 5 Text-figures.

I. Introduction.

This is the third of a small number of papers intended to serve as a basis for the study of the development of external form in *Forficula*. It is also hoped that they will promote the revision of the systematics of the Dermaptera as already explained (Henson, 1950).

II. The Neck.

In *Forficula* the neck, comprising the whole region between head and thorax, is so well developed that it is not altogether surprising that the question of its segmental value should have been raised (Verhoeff *in* Snodgrass, 1909). Crampton (1917), however, pointed out that the embryological evidence is absolutely against any suggestion that either the neck (the so-called microthorax) or the thoracic intersegmental regions represent reduced segments. In the same paper he maintains that the intersegmental plates of the thorax are serially homologous with the plates of the neck. Combining the views of Crampton with those of Snodgrass (1935) it seems probable that in a generalised insect the neck sclerites consist of anterior and posterior ventral plates, anterior and posterior lateral plates, and left and right dorsal plates. Snodgrass furthermore considers it very likely that the intersegmental line between the labial and prothoracic segments passes between the two lateral cervical plates.

Forficula conforms almost exactly to this generalised condition, there being two ventral sclerites (fig. 1B, AVC, PVC), two lateral sclerites (ALC, PLC), and a single narrow dorsal sclerite (DC), which can readily be shown to be derived from paired right and left elements present in the nymph. Functionally the most important of these plates are the lateral cervicals, since it is upon these that the head is movably articulated.

From both the morphological and functional standpoints a comparison with the corresponding regions in *Blatta orientalis* L. is most instructive. Here, as in *Forficula*, the lateral cervicals are large and serve for the articulation of the head, but the two ventral sclerites are relatively small and much less well developed. The anterior lateral plate (fig. 1A, ALC) is somewhat pointed towards its front end where it articulates with the condylar projections of the cranium, but its line of articulation with the posterior plate (PLC) is broad and hinge-like. In *Forficula* the posterior lateral cervical is much as in *Blatta*, but is securely wedged between the prothoracic sternum, the lateropleurite and the posterior ventral cervical (fig. 1B). The anterior lateral cervical, however is much more specialised. Much of it is rolled upon itself and deeply sunk into the cavity of the neck, where it forms a rod-like apodeme articulated at its front end to the cranial condyle and bent posteriorly into a hook-like process which carries muscle attachments. In its middle regions the plate remains superficial and broadly hinged to the posterior lateral cervical. The whole forms a most efficient system of levers, which allows the head to be uplifted to take full advantage of the prognathism of the mouth parts.

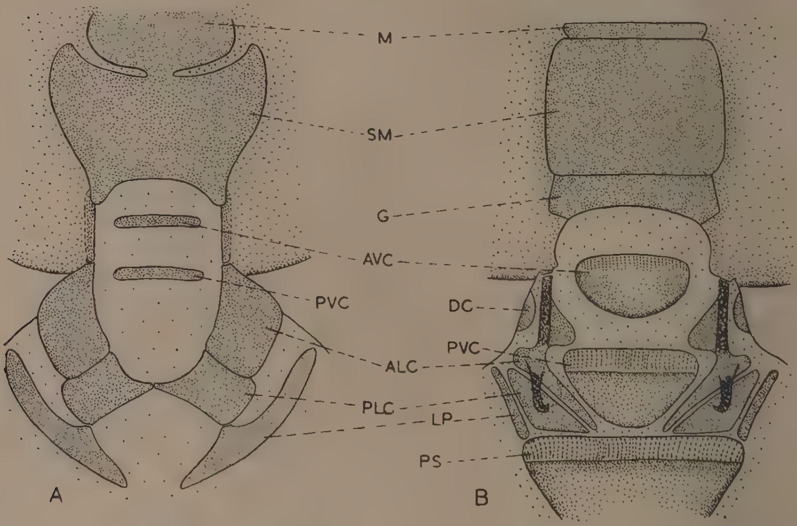

Fig. 1.—A, Cervical sclerites of *Blatta orientalis* L. from below. B, same in *F. auricularia* L. ALC, anterior lateral cervical; AVC, anterior ventral cervical; DC, dorsal cervical; G, gular; LP, lateropleurite; M, mentum; PLC, posterior lateral cervical; PS, prothoracic sternum; PVC, posterior ventral cervical; SM, sub-mentum.

Attention may be directed to the curious simulation of serial homology shown by the prothoracic sternum and the ventral cervicals. Each has a raised anterior ridge of the same form and each is flanked by a similar triangular sclerite, i.e., trochantin, posterior lateral cervical, and anterior lateral cervical respectively. These resemblances, from the point of view of classical morphology, are of course superficial, but their true appreciation may be significant in the realms of causal morphology. Certainly our knowledge of the genesis of segmentation is not great enough to dismiss such a possibility.

The anatomy of the neck sclerites in *Forficula* is evidently very similar to that of *Echinosoma*, *Arixenia* and *Hemimerus*, as illustrated by Crampton (1926), although his interpretations and nomenclature are not very consistent. In his figures Crampton labels the posterior element of the labium "gular" and the ventral cervicals "intersternite" and "presternite." In the text he abandons " presternite," and considers the posterior cervical to be " intersternite " and the anterior cervical to be " gular." In his 1928 paper " gular " is once more used for the posterior element of the labium, this no doubt being the more acceptable interpretation.

III. The Thoracic Tergites.

The dorsal plates of the thorax are the usual pronotum, mesonotum and metanotum. In many insects the mesonotum and metanotum can be subdivided into alinotum and postnotum, but in *Forficula* a postnotum is present only in the metathorax.

In view of the account given by Snodgrass (1935), it is of some interest to determine the extent to which *Forficula* conforms to the general principles underlying the relationships between the thoracic sclerites and the original body segmentation. Following Snodgrass, fig. 2A represents the primary segmentation with segmental tergites (PT), intersegmental membranes (ISM) and attached segmental muscles. In fig. 2B the sclerotisation of the intersegmental membranes produces the acrotergites AC, each with antecostal suture (AS) and internal antecostal ridge (AR). In the abdomen a typical secondary segmentation is established by the fusion of each acrotergite with the primary tergite immediately behind it (fig. 2C, to the left). The typical arrangement in the thorax is, however, rather different. The pronotum (fig. 2C, PN) is the primary tergite of its segment, the dorsal cervical (CV) presumably representing the acrotergite properly belonging to it. The mesonotum is a typical secondary tergite, its anterior acrotergite having an enlarged antecostal ridge forming the first phragma (1.PH). The acrotergite next following enlarges to become a separate postnotum (MST), the internal ridge of which is the second phragma (2.PH). The metanotum is the third primary tergite, whilst the next succeeding acrotergite forms the metathoracic postnotum (PST) carrying the third phragma (3.PH). The first dorsal abdominal plate (1.AB) is thus also a simple primary tergite.

In *Forficula* (fig. 2D) the arrangements conform fairly well to this general plan. The pronotum (PN) represents the primary tergite of its segment and is a large plate with steeply depressed anterior margin moulded to the form of the neck. The membrane (ISM) along its hinder margin is of course the secondary intersegmental ; it is doubly folded, and although extensible is chitinised to a certain extent. The mesonotum (MS) is, as usual, a typical secondary tergite carrying the large first phragma (1.PH). The next acrotergite with the second phragma (2.PH) is atypical in that it does not form a separate postnotum but is fused to the metanotum (MT), which is thereby converted into a typical secondary tergite. The acrotergite next following (PST) bears the small third phragma (3.PH) and is a typical metathoracic postnotum. It is lightly fused to the metanotum in its median region and to the first abdominal tergite laterally. The dorsal plate of the first abdominal segment (1.AB) is again a simple primary tergite. This condition with only one postnotum, the metathoracic, is usual in insects in which the hind wings are the principal organs of flight such as the Orthoptera and Coleoptera.

In *Forficula* the metathoracic postnotum is definitely bipartite, i.e., composed of two lateral halves each with a phragma and connected together by a narrow median bridge. In *Blattella* the corresponding structure is completely

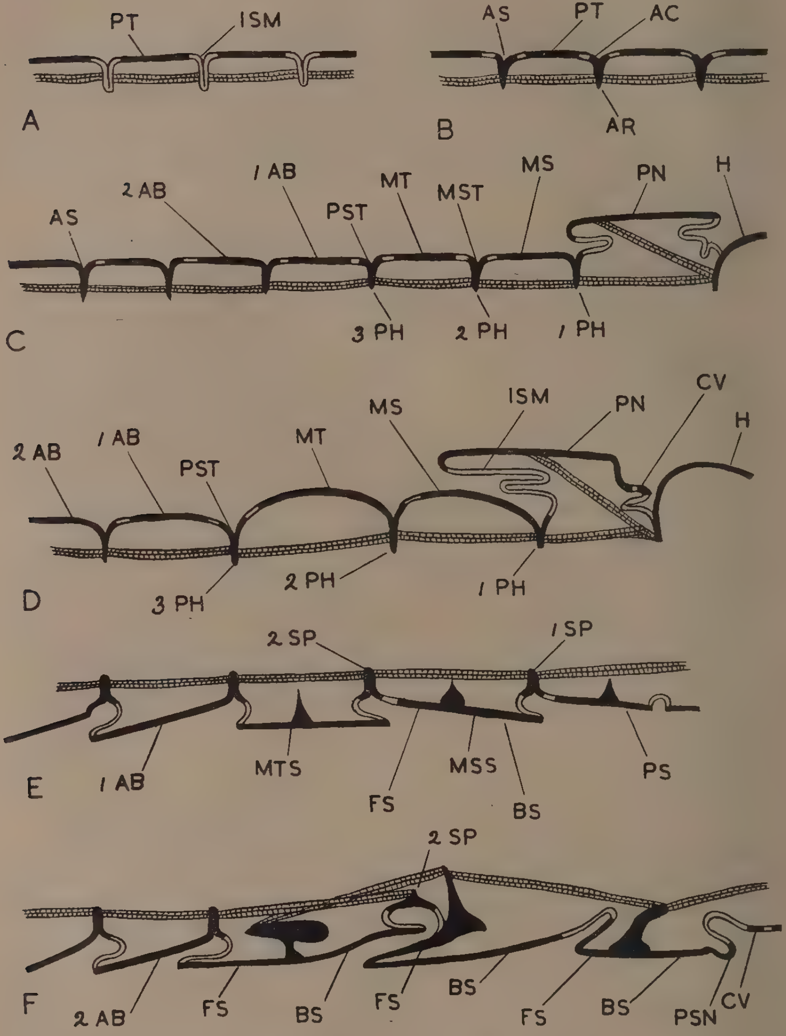
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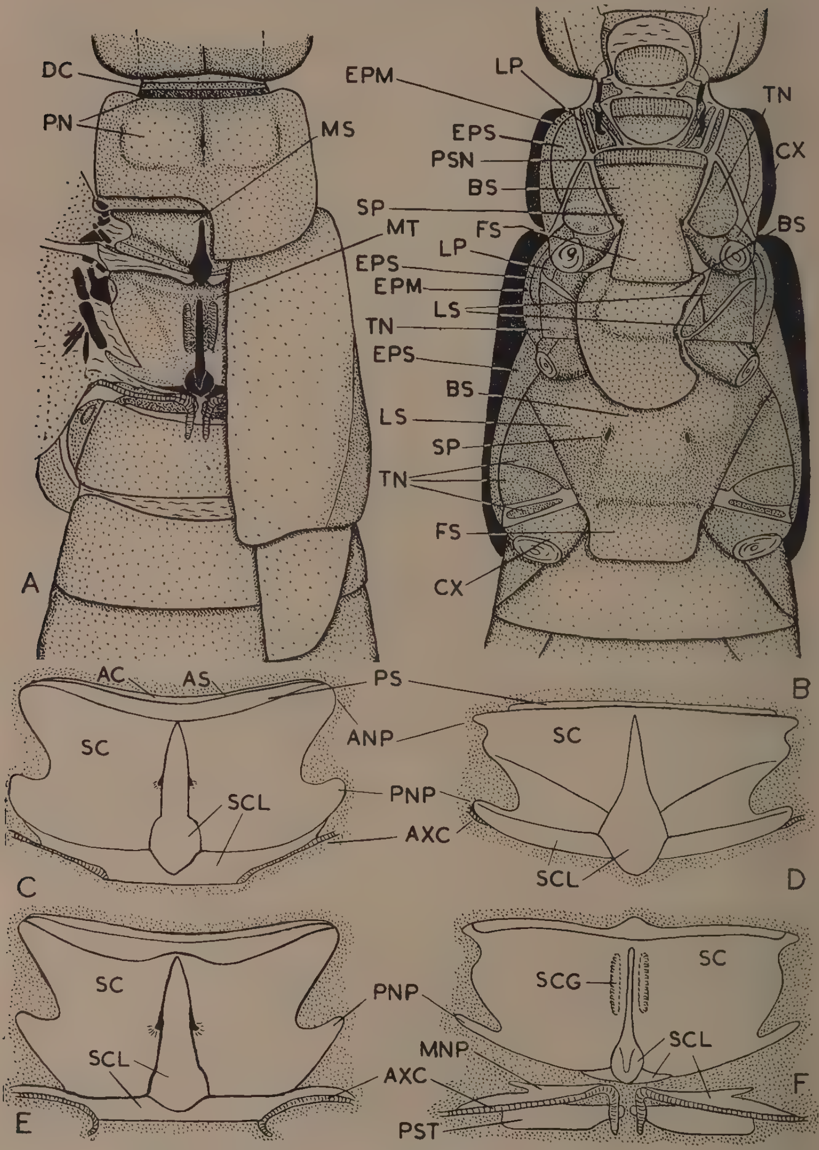
Fig. 2.—Relations of tergites and sternites to body segmentation. A, B, C, Generalised arrangement of tergites (after Snodgrass). D, thoracic tergites of *F. auricularia.* E, generalised arrangement of sternites (after Snodgrass). F, thoracic sternites of *F. auricularia.* 1.AB, first abdominal segment; 2.AB, second abdominal segment; AC, acrotergite; AR, antecostal ridge; AS, antecostal suture; BS, basisternum; CV, cervical sclerite; FS, furcasternum; H, head; ISM, intersegmental membrane; MS, mesonotum; MSS, mesosternum; MST, meso-postnotum; MT, metanotum; MTS, metasternum; 1.PH, 2.PH, 3.PH, first, second and third phragmata; PN, pronotum; PS, prosternum; PSN, presternum; PST, meta-postnotum; PT, primary tergite; 1.SP, 2.SP, first and second spinasterna.

separated into two halves, the so-called lateral yoke plates. Furthermore, as already mentioned, the dorsal cervical sclerite in the nymph of *Forficula* is also separable into right and left halves. Crampton (1917) gives a figure of *Japyx* in which the dorsal cervicals and the intersegmental plates of the thorax are represented as paired elements. There is evidently a strong case for regarding the acrotergite as being derived from paired rudiments, at least as far as the thorax is concerned.

In a generalised insect mesonotum or metanotum various regions such as scutum, scutellum and prescutum can be distinguished (*v.* Snodgrass 1935). In *Forficula* there is no doubt that this basic morphology underlies the form of the mesonotal and metanotal plates, but exact interpretation is not easily achieved. As in the case of the neck sclerites the best results have been obtained by comparison with the corresponding parts in *Blatta.* (fig. 3). Here both alary segments (C,E.) are much alike, the acrotergite is developed as a well defined prescrutum (PS), whilst the scutellum (SCL) is produced far forwards almost cutting the scutum (SC) in half. The scutellum itself is differentiated into a median body and posterior wings separated from each other by a shallow groove. In the metanotum (E) the wings of the scutellum are continued outwards into the basal region of the flying membrane and the axillary cords (AXC) extend towards the median line, where their tips project freely from the margin of the scutellum.

In *Forficula* (fig. 3, A, D, F) the notal plates are developed in a particularly characteristic fashion. In the metanotum (F) comparison with *Blatta* (E) indicates that the body of the scutellum has contracted anteriorly into a narrow prong and condensed posteriorly to form an upraised tongue, which appears to be the only part normally recognised as scutellum in systematic work. The prong-like portion lies in the bottom of a deep median groove (SCG) in the scutum furnished with closely set transverse ridges. These ridges articulate with tooth-like structures on the underside of the tegmina, which are thereby securely locked in position when at rest. Two similar but smaller depressions are to be found in a corresponding position on either side of the scutellum in *Blatta* (E). The wings of the scutellum (SCL) seem to have become separated into tiny portions still continuous with the body and larger portions (MNP) lying along the axillary cords (AXC). These latter are very conspicuous and have passed inwards right up to the median line, where their projecting tips become very prominent. The plates MNP were noted by Snodgrass (1909) and called by him " posterior arms of the metanotum " ; their interpretation as scutellar wings depends on their relations to the axillary cord, more especially in view of the form of these parts in *Blatta.*

In the mesonotum (fig. 3, A, D) the body of the scutellum is not quite so contracted as in the metanotum, but its posterior upraised tongue is well marked and projects upwards between the bases of the tegmina when these are in the closed position. The posterior half of the scutum is strongly depressed and inrolled to form a deep gutter. The lateral wings of the scutellum present a considerable problem of interpretation. In some specimens a faint line can be traced from the posterior notal process to the body of the scutellum, presumably marking off the anterior boundary of the scutellar wings. The axillary cords of the tegmina terminate near the outer margins of the notum just behind the posterior notal process, but in view of their condition in *Blatta* this is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D
SC
SC
SCG
PNP
SCL
SCL
MNP
AXC
F
E
PST

FIG. 3.—A, Thoracic region *F. auricularia*, dorsal view. B, same, ventral view. C, mesonotum of *B. orientalis*. D, same, *F. auricularia*. E, metanotum of *B. orientalis*. F, same of *F. auricularia*. AC, acrotergite ; ANP, anterior notal process ; AS, antecostal suture ; AXC, axillary cord ; BS, basisternum ; CX, coxa ; DC, dorsal cervical sclerite ; EPM, epimeron ; EPS, episternum ; FS, furcasternum ; LP, lateropleurite ; LS, laterosternite ; MNP, metanotal plates ; MS, mesonotum ; MT, metanotum ; PN, pronotum ; PNP, posterior notal process ; PS, prescutum ; PSN, presternum ; PST, postnotum ; SC, scutum ; SCG, scutal groove ; SCL, scutellum ; SP, sternal pit ; TN, trochantin.

probably a reduction from a more primitive condition in which they passed further in towards the middle line. In fact Pantel (1917) mentions that some *Diplatys* and some *Echinosoma* have their axillary cords extending right up to the point of the scutellum, as in the metathorax. It seems reasonable to suppose therefore that the whole of the posterior margin of the mesonotum is really made up of the wings of the scutellum.

In both the meso- and metathorax the anterior margin of the notal plate is steeply depressed and carries the usual phragmata. In neither is there a clearly defined antecostal suture, but the position of the phragmata indicates that the suture is very close to the extreme anterior margin and therefore that the greater part of the anterior flange is really prescutum.

IV. The Thoracic Pleurites.

According to Snodgrass (1935) the simplest form of pterygote pleuron is a single large chitinised area surrounding the coxa (fig. 4A). In further development the pleural apodeme is formed, the corresponding external suture separating epimeron (fig. 4B, EPM) and episternum (EPS). These plates then tend to separate off various independent sclerites such as trochantin (TN), laterosternite (LS), lateropleurite (LP), basalare (BA) and subalare (SA). The anterior corner of the scutum may be produced downwards to meet the episternum and is then known as prealare (PR).

A generalised forficulid pleuron is shown in fig. 4C. Episternum and epimeron are present, with the usual pleural suture, but the plates are distorted in such a manner as to bring the wing process (WP) far forwards. The trochantin (TN) is a large sclerite turned ventrally to give the coxa a ventral rather than an anterior articulation. The lateropleurite (LP) is present as a more or less independent sclerite, whilst the laterosternite (LS) is always recognisable although fused to the sternum except in the mesothorax.

In the prothorax (figs. 3B, 4D) the epimeron and episternum are large and the pleural suture very obvious. The pleural apodeme is a strong internal ridge, which gives rise to a long slender pleural arm (PLA) which crosses the body cavity to join the sternal furca. The trochantin is large and has a strongly inturned ventral edge. The laterosternite is fused to the sternum but the lateropleurite is a completely separate entity. That this latter is really a part of the episternum is clearly shown by the fact that it is not separated in nymphal stages (also Pantel, 1917), or, according to Crampton's (1926) figures, in *Hemimerus*, *Arixenia* or *Echinosoma*. There is no trace of the oblique suture across the episternum and epimeron mentioned by Pantel (1917) as present in *Allostethus* and related genera.

In the mesothorax all the main pleural plates are recognisable (figs. 3B, 4E). The episternum and epimeron are long and narrow and more strongly directed forwards than in the prothorax. The pleural suture is prominent but ends rather vaguely at its front end, where there is only the merest indication of a wing process. The pleural arm is very long and slender and extends to the sternal furca. The attachment of the tegmen is very weakly developed; on the shoulder of the wing close to the tegula (TG) is a small prealare (PR) situated between the point of the mesoscutum and the upper end of the lateropleurite. Pantel (1917) interpreted this sclerite as a wing axillary and then

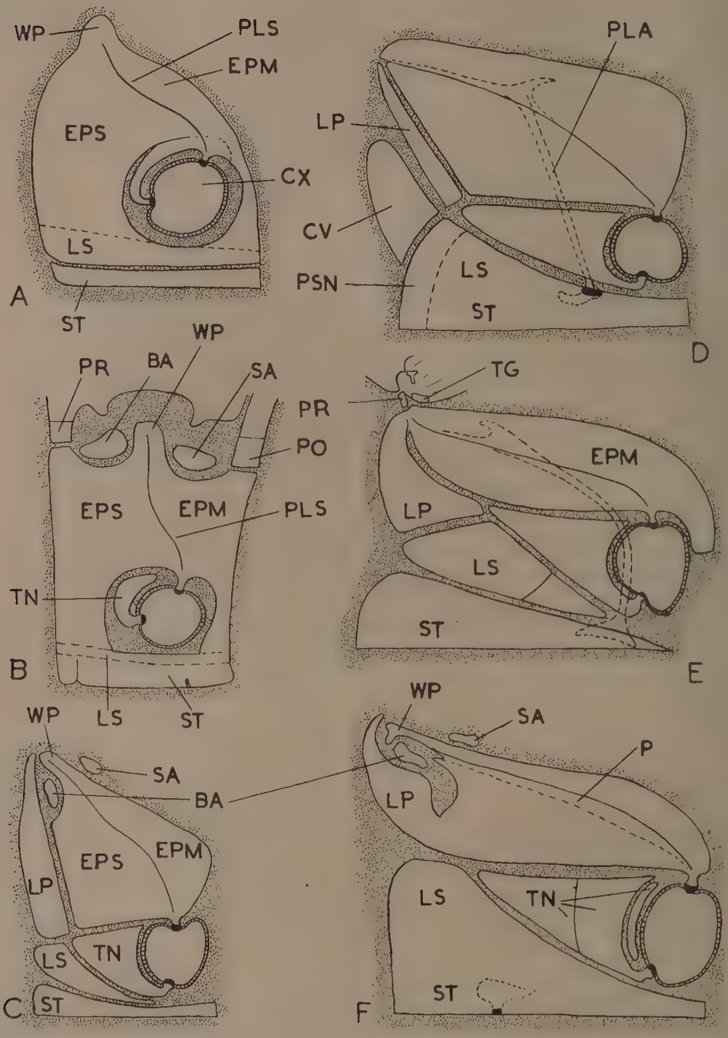
WP
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FIG. 4.—A, B, generalised pleural plates of pterygote insects (after Snodgrass). C, generalised forficulid pleuron. D, E, F, pro-, meso-, and metapleuron of *F. auricularia.* Internal apodemes shown as dotted lines. BA, basalare ; CV, posterior lateral cervical ; CX, coxa ; EPM, epimeron ; EPS, episternum ; LP, lateropleurite ; LS, laterosternite ; PLA, pleural arm ; PLS, pleural suture ; PO, postalare ; P, pleural ridge ; PR, prealare ; PSN, presternum ; SA, subalare ; ST, sternum ; TN, trochantin ; TG, tegula ; WP, wing process.

used it as evidence for the existence of a third notal process. The lateropleurite is not completely divided off from the episternum but the laterosternite is a separate plate. Both laterosternite and trochantin (fig. 3B) are vaguely divisible into separate parts.

In the metathorax (figs. 3B, 4F) the epimeron is reduced and the forward slope of the sclerites is very pronounced. The pleural suture is deep, giving a very strong pleural ridge, but there is no pleural arm connecting to the sternal apodeme. The wing process is long and flanked by basalare (BA) and subalare (SA). The lateropleurite is distinguishable but remains attached to the episternum at its ventral end. The laterosternite is fused to the sternum as in the prothorax. The trochantin again has a thickened ventral edge projecting under the sternal plate and is definitely divisible into three separate sclerites.

V. THE THORACIC STERNITES.

In insects generally the arrangement of the ventral segmental plates is essentially similar to that of the dorsal plates. In the abdomen primary sternites and acrosternites fuse to form typical secondary sternal plates but in the thorax they remain free, the former as eusternites and the latter as spinasternites (fig. 2E). The eusternites develop large paired sternal apodemes whose origin is shown externally by sternal pits (fig. 3B, SP). The part of the eusternum in front of these pits is the basisternum and the part behind them the furcasternum. The anterior edge of the eusternum may be strongly reinforced or otherwise marked off as a presternum. The spinasternites, of which there are normally two, carry a median apodeme, the spine. As a general rule the thoracic sterna overlap from behind forwards and not from in front backwards as in the abdomen ; the metasternum overlaps both ways (fig. 2E).

In *Forficula* (figs. 2F, 3B) the arrangement of the sternal plates differs appreciably from the generalised condition but is readily derived from it. In the prothorax the sternum consists of fused eusternum and laterosternite. It is strongly differentiated into presternum (PSN), basisternum (BS) and furcasternum (FS). The latter hangs like an apron over the mesosternum and its lateral edges are strongly inturned, reinforcing the furcal arms and bringing the sternal pits far to the side. The true posterior margin of the furcasternum is reflected internally and overlapped by the larger visible portion. There is no acrosternite, and hence no spina, between the prothorax and mesothorax (fig. 2F).

The mesosternum is a large oval plate which does not incorporate the laterosternites (figs. 3B, 2F). There is no presternum, but basisternum and furcasternum are strongly developed. In surface view the furcasternum and sternal pits cannot be seen because the whole of the furcasternum is folded beneath the basisternum (fig. 2F). The furcal arms are relatively enormous. The second spinasternum, complete with spina, is present, but is overlapped from behind by the metasternum and both are then covered by the mesosternum.

The metasternum is very large with broad wings which represent the laterosternites. The sternal pits are far forwards, the whole furcasternum being visible and not folded beneath the basisternum as in the pro- and mesothorax. The furcal arms, of characteristic shape (fig. 2F), are not connected to the pleural ridge by pleural arms.

VI. The Thoracic Legs.

The form of the legs in the Dermaptera is highly characteristic of the group. Each leg (fig. 5) consists of the usual parts, coxa, trochanter, femur, tibia, tarsus and pretarsus. Femur and tibia are approximately equal in length. The tibia is "elbowed" proximally, and in flexion fits into a deep groove on

Mensuration Table (*Forficula auricularia* L.).*

Measurements in units of 10μ.

M. = male. F. = female.

Antennal segments.	No. of specimens.		Observed range.		Mean.		Standard deviation.		Variability co-efficient.	
	M.	F.	M.	F.	M.	F.	M.	F.	M.	F.
Segment 1	21	17	48–63	49–63	55·0	55·0	3·78	2·89	6·88	5·26
2	21	20	54–67	52–63	57·7	57·9	3·61	2·43	6·27	4·20
3	21	22	56–72	56–66	62·3	62·0	3·59	2·65	5·78	4·28
4	21	22	59–72	59–68	64·3	65·0	3·38	2·59	5·25	3·99
5	21	22	64–76	62–72	68·1	69·0	3·39	2·65	4·99	3·85
6	21	22	60–72	64–73	65·6	67·3	2·75	2·24	4·23	3·33
7	21	22	62–71	62–72	65·3	66·9	2·51	2·75	3·86	4·12
8	21	22	56–67	59–72	62·3	64·7	2·96	3·08	4·76	4·79
9	21	22	48–57	50–63	52·5	55·3	2·70	3·31	5·13	6·00
10	21	21	35–43	36–45	37·9	40·2	2·04	2·68	5·41	6·66
11	21	21	22–29	24–30	25·8	27·1	1·74	1·97	6·78	7·30
Meriston III	21	21	29–40	27–36	31·9	31·7	2·71	2·51	8·50	7·94
Pedicel II	21	22	11–22	16–21	18·0	19·2	2·29	1·30	12·73	6·84
Scape I	20	22	60–73	59–69	64·5	64·6	2·85	2·60	4·44	4·02
Head										
Width	30	22	188–220	192–228	205	212	8·25	9·72	4·03	4·59
Pronotum										
Length (l.)	30	21	148–181	144–188	164	166	9·61	10·68	5·89	6·43
Width (w.)	30	21	172–216	179–226	193	199	11·86	13·10	6·14	6·56
Ratio (w./l.)	30	21	1·09–1·30	1·08–1·47	1·18	1·20	·045	·08	3·79	6·63
Anterior leg										
Femur	29	22	132–176	144–172	155	160	10·91	6·65	7·07	4·16
Tibia	29	22	148–197	157–188	170	175	11·25	8·15	6·60	4·66
Tarsus 1	28	21	62–77	60–82	69	69	3·94	5·13	5·77	7·35
,, 2	29	21	38–48	38–46	43	43	2·54	2·04	5·94	4·77
,, 3	29	21	54–67	55–67	62	63	3·17	3·02	5·13	4·82
Middle leg										
Femur	29	22	150–216	179–207	189	195	13·25	7·74	7·02	4·00
Tibia	29	22	138–207	176–195	183	187	13·45	6·58	7·38	3·52
Tarsus 1	29	21	71–92	72–91	80	81	6·64	4·36	8·32	5·38
,, 2	29	21	40–52	40–49	46	45	2·81	1·71	6·20	3·28
,, 3	28	22	56–71	58–71	65	66	3·42	2·82	5·26	4·28
Post. leg										
Femur	29	22	207–270	228–254	237	243	15·03	7·23	6·34	2·98
Tibia	29	22	197–260	220–254	232	226	13·19	9·01	5·68	3·82
Tarsus 1	29	21	102–137	106–132	114	116	8·23	6·39	7·20	5·47
,, 2	28	21	44–56	47–54	49	50	2·94	1·91	5·98	3·84
,, 3	29	21	59–81	64–78	72	73	4·42	3·78	6·21	5·22

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* The author gratefully acknowledges the very considerable help given by Mr. W. D. Hincks, M.Sc., in making these measurements.

the ventral surface of the femur. The tarsus is three-jointed; the first joint is much the longest, the second is spatulate and the third normal. The second joint articulates with the third about the middle of its length on its upper surface. The pretarsus consists of two large claws only; there is no empodium.

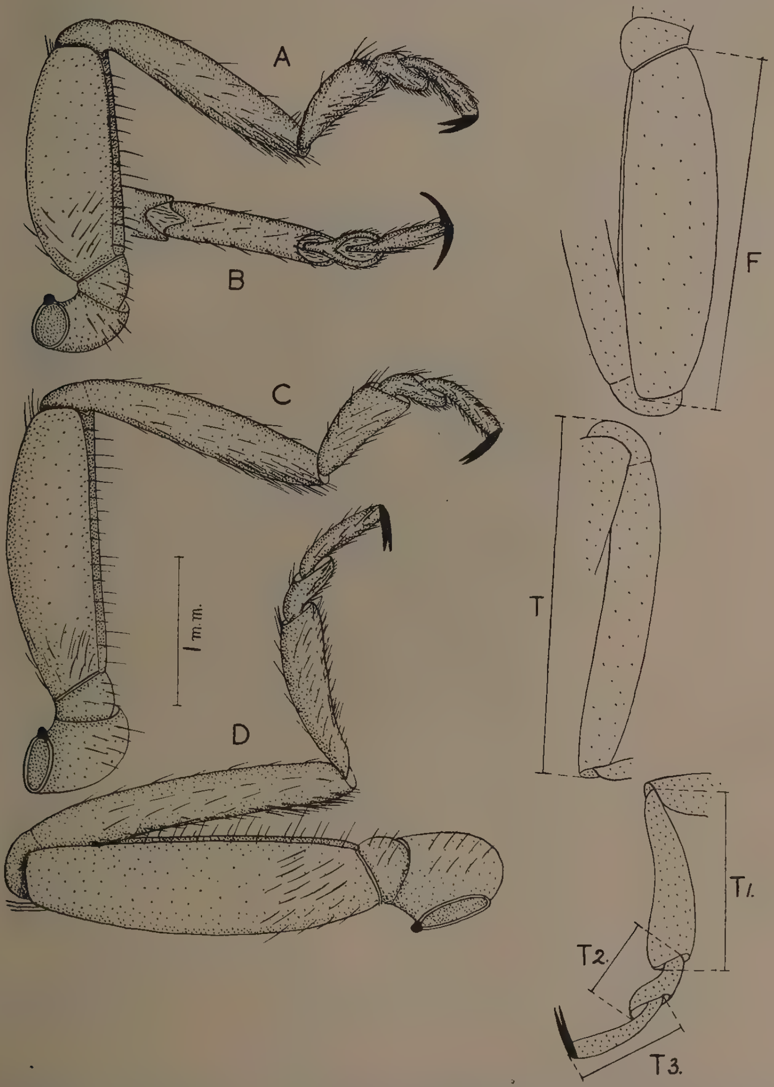

FIG. 5.—Legs of *F. auricularia*. A, fore leg. B, hind tarsus from above. C, middle leg. D, hind leg. Lengths of leg joints, as given in the table, shown by F, femur; T, tibia; T1, T2, T3, tarsal joints.

VII. NOTES ON MENSURATION.

One of the two main objectives in the writing of this paper was to provide information which would promote the revision of the systematics of the Dermaptera as a whole. In view of the fact that in certain insect groups characters such as relative lengths of antennal segments, relative lengths of leg segments, and proportions of the pronotum are found to be " useful " in the identification of species, it was thought that information on these points would be of value. The data are presented in tabular form.

For systematic purposes mensuration can be used effectively only when a sufficient body of information is available. The methods are described in sufficient detail by Simpson and Roe (1939). In brief it is as follows: If, in the case of an unknown specimen, any individual measurement is more than three times the standard deviation from the mean of the organ in question, it is likely that the specimen being considered is different in race or species from those with which it is being compared. This, of course, becomes more certain if a large number of different organs are measured and found so to differ. In this latter case it may be sufficient to use a criterion of two and half times the standard deviation from the mean. It should be noted that the converse conclusion is not to be drawn. If all measurements fall within the limits mentioned it does not prove that the specimen is the same species—it merely indicates that it could be.

The significance of the data in respect of the antennal segments has been discussed in a previous paper (Henson, 1947).

The width of the head was measured at its widest part, just behind the compound eyes. The antennal segments were measured between the two constrictions at either end. The limits used in the measurements of the leg joints are shown in fig. 5. In the case of the pronotum the greatest width and the length in the mid-line are given.

VIII. SUMMARY.

1. The external morphology of *Forficula auricularia* L. can readily be interpreted in terms of the general theoretical considerations presented by Snodgrass (1935).

2. The neck sclerites are directly comparable with those of *Blatta*, and consist of anterior and posterior ventral plates, anterior and posterior lateral plates, and left and right dorsal plates—fused in the mid-line in the adult.

3. The thoracic tergites are " normal " except that there is only one postnotum, the metathoracic, as in Orthoptera and Coleoptera. As in the case of other dorsal intersegmental plates, it is bipartite and corresponds to the yolk plates of *Blattella*.

4. The notal plates are divisible into scutum and scutellum. The position of the alary cords and comparison with *Blatta* strongly indicate that both body and wings of the scutellum are present.

5. The pleurites comprise episternum, epimeron, lateropleurite, trochantin and laterosternite.

6. The sternal plates have typical subdivisions but there is only one spinasternite and in the mesothorax the furcasternum is completely enclosed beneath the basisternum.

7. A mensuration table is given for many parts of the body in *F. auricularia*. Similar tables for other species would be valuable contributions to Dermapteran systematics.

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THE DEVELOPMENT OF IMAGINAL BUDS IN THE HEAD OF *PIERIS BRASSICAE* LINN. (LEPIDOPTERA).

By Y. E. E. Eassa, Ph.D., B.Sc.

(*Department of Zoology, University of Sheffield.*)

Manuscript received 13th October, 1952.

(Read 3rd December, 1952.)

With 1 Plate and 3 Text-figures.

This account is part of a comprehensive investigation which has been made into the developmental changes which take place in the head during the growth of the caterpillar of *Pieris brassicae* and its subsequent metamorphosis.

Attention is here directed to the development of the adult appendages from imaginal buds which grow throughout larval life and to the contribution which some of the growth centres make to the adult head capsule.

There is a voluminous literature dealing with this topic in insects generally, and reference will be made only to the outstanding works. Weismann (1864) in his account of the post-embryonic development of muscid Diptera related the embryonic islands of cells in the body of a holometabolous larva to ultimate adult structures. He also threw light on the important histolytic and histogenic changes which take place during pupation and, through this, made it clear that, while some adult structures are derived from embryonic cells of the larva, some part of the functional larval tissue continues without change to function in the adult. In 1866 Weismann also showed that in *Corethra* the thoracic limb rudiments arise as ectodermal infoldings after the last larval moult, just before pupation. This position was elaborated further by Ganin (1869; 1876), who demonstrated many imaginal rudiments in addition to those described by Weismann. With Dewitz (1878), he agreed that in metamorphosis there was something akin to an extension of embryonic life. Kunckel d'Herculais (1875), Viallanes (1882), van Rees (1888), Kovalevsky (1887), Pratt (1897) are others of the last century who contributed to this field of investigation.

A separate reference, however, must be made to Gonin, who in 1894 made a study of *Pieris brassicae*. Gonin demonstrated the relation between the larval leg and the imaginal structure within it, the larval appendages being the points of departure of imaginal growth inwards. He then proved similar relations between larval antennae, maxillae and labial palpi and the adult counterparts. He noted the absence of any imaginal structures within the caterpillar's mandible and labrum, and he pointed out, quite correctly, that an imaginal disc developed as a forerunner of the pupal crest. In principle Gonin's contribution is valuable; his results summarised by Packard (1898) are, however, incomplete in some details and in some respects incorrect.

In 1911 Perez studied adult limb development in *Phytonomus adspersus* (Coleoptera), and found that, in the limbless larva, the imaginal structure developing within the skin is connected with a larval sensillum. This association between the larval sensillum and the developing adult appendage within forms the starting point for a further searching inquiry by Keilin (1915) into the Diptera Cyclorrhapha. In these it was found that sensilla occur as relics of the larval appendages in the places where the imaginal discs of these appendages take their origin, and where their peripodial membranes open at the hypodermis by a pore underneath the larval cuticle.

In the present work the development of the adult appendages has been followed through the larval instars into the pupal stage. Attention has also been given to the growth of the labrum and the pupal crest. It is shown that certain of the growth processes described involve the head capsule in changes from the larval to the adult condition. Considerations of morphology bring with them the related ones of terminology. Attention may, therefore, be drawn to Hinton's (1947) criticism of the terminology of Snodgrass (1928, 1932, 1935 and 1947), and to the detailed analysis made of these matters by Short (1951). In this paper it has been deemed advisable, without prejudice, to adopt the terminology of Snodgrass on the grounds that the disputes on terminology are not relevant to the main issue of this contribution. Most of the work was done by serial sections, but when the individual imaginal rudiments were big enough, dissections of the head were made, and measurements then taken of them. These measurements in the ultimate can only be approximations, but since they were made at intervals between moults, they throw some light on the steady and continuous growth of the adult rudiments within the period of an instar.

The Antenna.

The adult antenna begins development in the first larval instar. It is first recognised as a slight hypodermal cell-thickening, surrounding the sense cells and trichogens of the sensilla at the tip of the larval organ. It then undergoes an increase in size by the mitotic activity of these lateral cells, leaving its sense cells at the tip (fig. 1*a*). The surrounding hypodermis in connection with the growing bud becomes folded to form a peripodial membrane. Thus 24 hours after the beginning of the second instar the whole structure consists distally of sense cells and trichogens, and more basally of rapidly dividing small embryonic cells, this latter region being reflected into the tissue of the peripodial membrane, which leads in turn to the normal surrounding hypodermis. A well recognised tracheolar supply is seen to enter the antennal basal region.

In the third instar the most notable feature lies in the development of an invagination into the basal region of the hypodermal thickening (fig. 1*b*). This causes the antenna to present itself as a hollow structure, the base of which is almost filled with tracheoles and whose basal walls are reflected outwards as the peripodial membrane. Extension and folding of the peripodial membrane proceeds *pari passu* with the invagination just mentioned. At this stage there is an even sharper distinction than before between distal larval functional cells (trichogens and sense cells) and basal imaginal non-functional cells. The latter pass for a short distance into the peripodial membrane before this meets the hypodermis, with which it is continuous.

Fourth instar larvae show an increase in size of the antenna and its consequent basal projection into the head cavity. They also show an increase in the hollowness of the organ and in tracheolar supply. The distal sensory cell apparatus is still functional (fig. 1*c*).

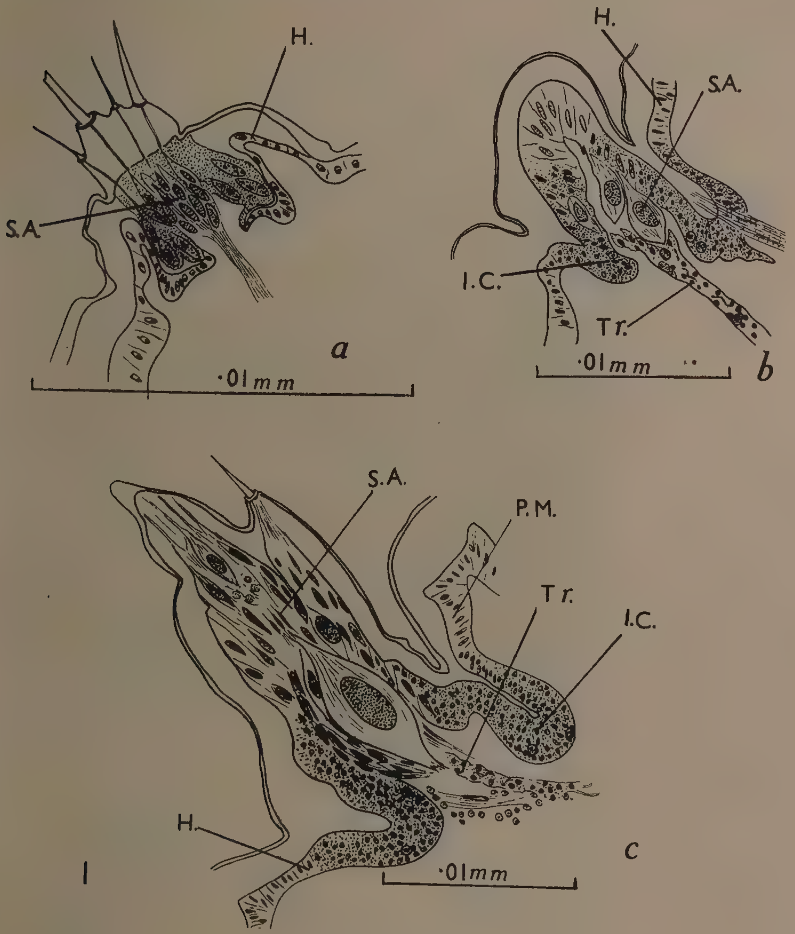


Fig. 1.—(*a*) L.S., larval antenna first instar. (*b*) L.S., larval antenna third instar. (*c*) L.S., larval antenna fourth instar. H., hypodermis; I.C., imaginal cells; P.M. peripodial membrane; S.A., sensory apparatus; Tr., tracheolar cells.

The fifth instar must for convenience be divided into the first six days of active larval life and the final three days constituting the prepupal period.

During the first of these two periods the most notable changes are those of size, and the sharp distinction between the outer region of the peripodial membrane whose cells are attentuated and the inner region of this same structure whose cells are minute, close packed and embryonic (Plate I, fig. 1). The increased size of the organ as a whole is later recognised by the fact that, while the now extensive peripodial membrane has carried the base of the organ deeply into the head cavity, the antenna itself is thrown into many transverse folds, showing that its growth has exceeded that of its surrounding membrane (Plate 1, fig. 2).

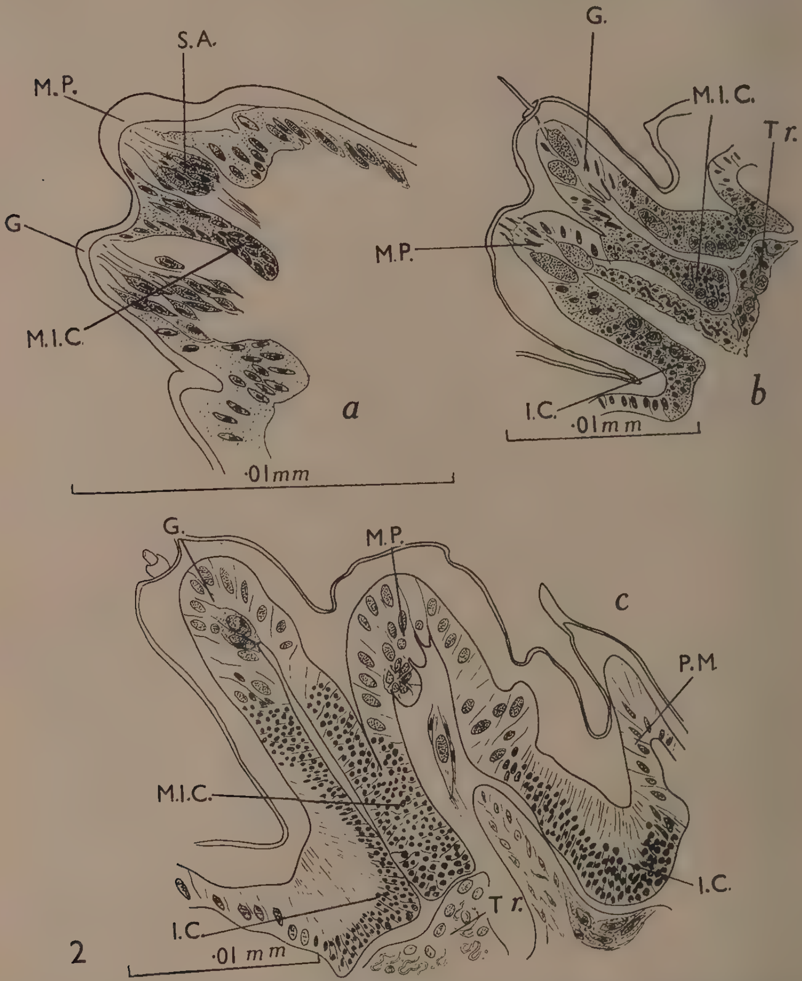


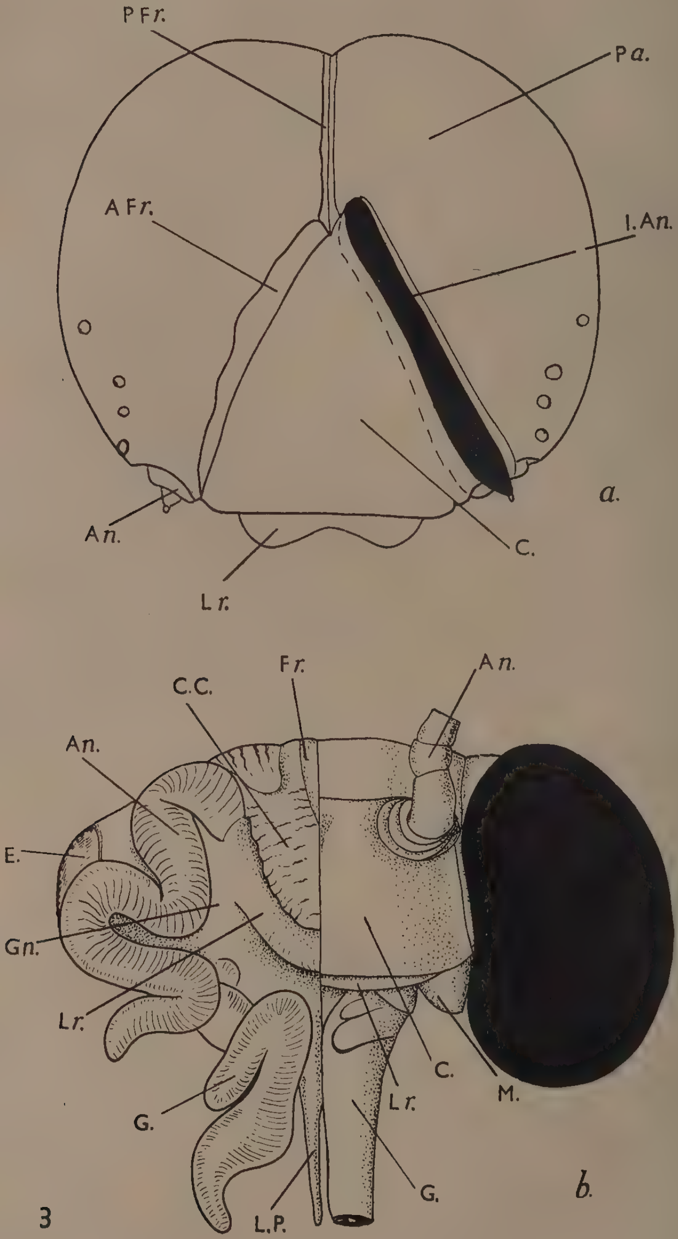
Fig. 2.—(*a*) L.S., larval maxilla second instar. (*b*) L.S., larval maxilla third instar. (*c*) L.S., larval maxilla fourth instar. G., galea; I.C., imaginal cells; M.I.C., median imaginal cells; M.P., maxillary palp; P.M., peripodial membrane; S.A., sensory apparatus; Tr., tracheolar cells.

The basal embryonic cells of the peripodial membrane are important, since they form a separate imaginal rudiment from which part of the adult head capsule will be formed. Early in this instar there can still be seen the terminal sensory cells as distinct from the embryonic cells below them. Towards the sixth day, however, there sets in a process of deterioration in this sense cell apparatus (Plate I, fig. 2), and as the prepupal period starts and the hypodermis separates from the cuticle, this degeneration proceeds apace. This sensory region becomes invaded by imaginal cells, so leaving the adult antennal rudiment with its distal cells little different from those in other regions.

Reference must now be made to the position within the head assumed by the antennal rudiment. At about the third day of this instar it can be seen to lie in line with the larval epistomal ridge (Plate I, figs. 3 and 4). The peripodial membrane of the antenna is peculiar in that it opens, not by a pore at the point of origin, but by a long slit which runs under the head cuticle parallel to the epistomal ridge of the head capsule (Plate I, fig. 3). It is along this slit, which runs along the whole length of the antennal rudiment, that the antenna will be disclosed at the moult. Therefore by growth of the adult antenna from the site of its origin in the larval organ, its base is carried to a point high up on the head well lateral to and above the clypeus. This point, the limit of ingrowth of the imaginal bud, is the site of the base of the pupal appendage (fig. 3*a*, 3*b*). At the fifth day the longitudinal slit of the peripodial membrane of the antenna opens out along the whole of its length, so bringing the antenna to a superficial position, but still beneath the larval cuticle. It is now still in line with the position it occupied in the larval head before its release. Later in the prepupal period it becomes coiled on itself as it stretches under its confining larval cuticle. Fig. 3*a* shows it in its larval and Fig. 3*b* in its prepupal and adult positions. Its base, or point of attachment to the head, has shifted from the original larval position to a new place high up on the head dorsolateral to the clypeus. This shift is the product of growth of the imaginal antennal rudiment, for the more it grew, the higher up was the antennal base pushed along the epistomal groove to its new final position. At the stage now reached in this description, the peripodial membrane becomes a little thicker because of some contraction of its tissue following the release of the antenna from within it.

An important result ensues from the change of position of the antennal base to its new prepupal and subsequent adult condition. The head surface between the larval and the prepupal antennal base is provided from the substance of the peripodial membrane. This latter unfolds, and adds its substance to the genal area of the head capsule. We note thus a change in position of the antenna and a new form of the head capsule. Both these new features have been determined by (*a*) the ingrowth of the antennal base during larval life, (*b*) the elongated opening of the peripodial membrane, in line with the epistomal ridge, and (*c*) the part played by the peripodial membrane in contributing to the genal surface of the pupal head capsule as the antennal base is carried up the head from its original larval position near the mouth. The significance of the imaginal cells in the wall of the antennal peripodial membrane will now be clear.

The association of the antennal imaginal bud with larval sensilla was not remarked upon by Gonin (1894), nor was the contribution made by the peri-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3

podial membrane to the head capsule. The method by which the antenna attains its ultimate position on the head and the consequences deriving from it appear to be reported here for the first time.

The Maxilla.

In the larva there is a small maxillary palp, and median to this the structure commonly called the " free lobe," thought by some to be galea and by others lacinia. Since the hypodermis of the " free lobe " in association with its terminal sensilla is destined to form the adult galea it seems reasonable to call it the larval galea.

In the first instar adult development is already beginning. Beneath the larval galea and the palp a definite hypodermal thickening occurs. Distally in each of these regions the cells, mostly sensory, are large and specialised for larval functions. The stipital hypodermis as yet shows no special feature of development. Towards the end of this instar the hypodermis between the galea and the palp begins to turn inwards to form a median maxillary fold. In the second instar (fig. 2*a*) the development begun in the first instar proceeds and tracheoles can now be seen entering the basal maxillary cell mass.

In the third instar (fig. 2*b*) the median fold between the galea and palp deepens considerably. The cells composing it are small and seem to be in active division, and at the end of the second day the hypodermis beneath the palp and the galea has become shaped like two hollow glove fingers into each of which there pass many tracheoles. In each of these finger-shaped rudiments the distal cells are large and sensory, the lateral and basal cells much smaller and very close packed. These small cells are particularly noticeable at the inner basal region of the galea, in the base of the median fold and on the outer side of the palpal region. The hypodermis surrounding this complex is thrown into a peripodial fold as the rudiments pass deeper toward the larval stipital cavity. We may say at once that these groups of imaginal cells are the rudiments of the adult galea and maxillary palp. Of these the last mentioned is the smaller and remains so.

In the fourth instar there is no development of note except in the direction already indicated in the third.

In the fifth instar the galeal and palpal rudiments become more distinct from each other as the median fold deepens. They pass inwards and come to lie within the cavity of the larval stipes, and in so doing increase the depth of the peripodial membrane which began to develop earlier. During the third day of this instar the sensory cells at the tip of the galeal and palpal rudiments in contact with the larval cuticle begin to degenerate. Now, also, it is seen that the palpal cell rudiment is restricted in extent to a small cell thickening

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FIG. 3.—(*a*) Front view of larval head showing, on left, position of larval antenna compared with, on right, position of imaginal antenna in line with the epistomal ridge. The dotted line indicates the approximate course of the slit through which the antenna will ultimately be released, leaving the adult antenna with its base far removed from its original larval position. (*b*) Front view of head on left in prepupal condition after removal of larval cuticle and on right in adult condition. AFr., antefrons; An., antenna; C., clypeus; C.C., clypeal crest; E., eye; Fr., frons; G., galea; Gn., gena; I.An., imaginal antenna; L.P., labial palp; Lr., labrum; M., mandible; Pa., parietal; PFr., postfrons.

at the base of the palpal peripodial membrane. All the remaining imaginal tissue of this complex including the median fold goes to form the galea, and growth of its cells by continued cell divisions carries its basal parts inwards as far as the cardo adductor muscle of the larva. So rapidly does this galeal rudiment grow at this stage that it is thrown into transverse folds within its peripodial membrane, much as is the antenna at the same stage.

At the end of this stage a tracheal branch penetrates the maxillary rudiment ready to replace in the pupa the tracheolar supply mentioned above.

In the prepupal period of this fifth instar the peripodial membrane of the maxilla shrinks and so brings the imaginal structures to the surface under the larval cuticle, the galea long and folded on itself, the palp small. They are thus brought to a position in front of the stipes, the hypodermis of which thickens into an imaginal rudiment, out of which the complex adult stipes is formed.

Labium.

The first instar shows no prominent signs of imaginal development of the labium, the hypodermal cells at the tip of the larval palp being large sense cells and trichogens. Those lateral to this, except for their slight crowding and smaller size, differ little from the normal hypodermis.

The second and third instars disclose no change in this respect, except that the lateral cells form a thicker mass and tend to move inwards, so throwing the lateral hypodermis into a small fold, the beginning of a peripodial membrane. The palp is the only part of the larval labium with which is associated any imaginal development, except for cells at the base of the peripodial membrane, which probably form the adult labial basal plate.

Only in the fifth instar do prominent imaginal developments begin. At the end of the first day the peripodial membrane of the imaginal bud of the labial palp is well formed, and the rudiment itself is seen to be hollow from within. A process of evagination has thus begun, and into the palpal cavity formed there pass tracheoles similar to those found in the antenna and maxilla.

As the imaginal bud grows in size its base sinks inwards behind its larval cuticle. This causes the deeper inturning of the peripodial membrane around it. At the same time evagination from the base of the bud becomes more pronounced, and as the central cavity of the imaginal rudiment grows, a still richer supply of tracheoles passes into it. The tip of the imaginal rudiment is still composed of sense cells and trichogens and constitutes the sensory apparatus of the larval palp.

The imaginal rudiment of the palp is, at the third day, very large, and occupies most of the space within the larval labium (Plate I, fig. 7). Its peripodial sac is wide open beneath the larval cuticle, and its internal cavity is similarly widely open to the blood space within the labium. The junction of the peripodial membrane with the palpal rudiment consists of imaginal cells like those similarly placed in relation to the antennal rudiment. It seems probable that those cells play a part in forming the labial basal plate of the adult, though this is not certain.

Towards the end of the larval period in question the larval apical sense cells show signs of degeneration. When the cuticle is freed from the underlying tissues—in the prepupal period—the palps are already outside their peripodial membranes and ready to assume the positions and attitudes characteristic of the pupa.

It will now be seen that there is no special adult development for the spinneret. It is also to be noted that practically all the development of the large adult labial palps takes place during the fifth larval instar.

Labrum and Clypeus.

Early in the fifth instar two growing centres appear in the hypodermis of the labrum on either side of the middle line. Not until the fourth day of this instar, however, are these imaginal buds of the labrum readily discernible. At this time they begin to fold inwards. A day later each fold spreads out laterally so as to meet its fellow. Meanwhile the unmodified hypodermal cells of the labrum begin to degenerate. In their places the new cells take up their positions and come to form the new labrum. This latter, in the prepupal period, is a relatively short structure, and the degeneration of the larval cells in it is further hastened by phagocytosis.

At the fourth day of the fifth larval instar there arises a transverse band of actively dividing cells in the lower region of the clypeal hypodermis (Plate I, figs. 3 and 5). This grows rapidly so as to form an imaginal growth centre composed of a very large number of minute cells easily distinguished from normal larval hypodermal cells. Their growth is rapid, and soon involves, by spreading in all directions, the whole of the clypeal area. On the fifth day the clypeal hypodermis has increased in size so as to occupy an area far bigger than the overlying cuticle. It therefore folds inwards in its lower region so as to form a recess under a conical process (Plate I, fig. 6). This condition prevails into the prepupal period, when the removal of the larval cuticle discloses the thus folded clypeus. The conical process at pupation projects forwards and forms the pupal crest, the hypodermis of which ultimately provides for the greatly enlarged clypeus of the adult.

The Epicranium.

One of the most striking features by which the imaginal head capsule differs from the larval is the size of the occipital foramen. In the adult it is small and constricted, while in the larva it is a wide opening by which the cranium is broadly attached to the thorax behind it.

The most posterior larval head sclerite is the postoccipital, a narrow curved structure extending downwards on either side from the middle dorsal line to the posterior tentorial pits which are found at the posterior ends of the hypostomal ridges. This arrangement persists in the pupa except that the postoccipital sclerite is inflected so as to be invisible externally. In the pupal period, however, there occurs a growth of hypodermis between the frons and parietals in front and the postocciput behind. This extended hypodermis is responsible for the development of a sclerite, the epicranium, which has no counterpart in the larva.

By its introduction and a shrinkage of the postoccipital hypodermis to accommodate itself to this new growth the occipital foramen is carried backwards, the size of the postoccipital sclerite is reduced and the occipital foramen made smaller. On the narrower connection thus formed the head is pivoted on the thorax, and thus is made possible the wide range of head movements of which the adult is capable.

Mandible.

There is no imaginal development of the mandible, the cells of which undergo degeneration at the end of the fifth instar. The mandibles are left as immovable vestiges incorporated into the body of the head capsule (fig. 3*b*).

Growth of Imaginal Structures.

Within the confines of a single instar it was observed that the imaginal structures continued to increase in size. The cells of which they are composed remain small, and the inference that mitosis goes on between moults is supported by direct observation.

The measurement of the imaginal rudiments could not be taken in the first and second instars. In subsequent instars, because of foldings, such measurements as were made can only be accepted as approximations. They are given here to support the evidence that growth of imaginal structures continues between moults.

In instar 4 the antenna grows continuously in length from 0·06 mm. to 0·10 mm. and in instar 5 from 0·125 mm. to 0·953 mm. In instar 3 the maxillary rudiment grows from 0·006 to 0·009 mm., in instar 4 from 0·08 to 0·116 mm., and in instar 5 from 0·128 to 0·885 mm. The labial palpal rudiment is not measurable until the end of the first day of the fifth instar period. It then grows apace so that before the prepupal period it is 0·500 mm. long. Considerable increases in length occur during the prepupal period, but these are so confused with infoldings that measurements are not given.

Discussion.

Several interesting things emerge from this investigation. First, the structures within the head destined to form the adult head appendages arise as rudiments closely associated with their larval counterparts. Thus the adult antenna arises as a hypodermal thickening behind the larval antenna, the adult galea from behind the " free lobe " of the larval maxilla, the adult labial palp from hypodermis in close association with the corresponding larval structure. Since the adult mouthparts are deficient in certain respects, for instance, in functional mandibles, it is not surprising to find no adult rudiments in association with these organs. We can, therefore, add a developmental criterion to that already provided by comparative anatomy for the establishment of correct homologies of the mouthparts of Lepidoptera.

With the development of imaginal buds of the head appendages there occurs in each case a folding of the hypodermis to form the peripodial membrane. This is usually regarded as undergoing a process of contraction and shrinkage at the end of larval life, its purpose having then been fully served. In this case it has been shown that the antennal peripodial membrane makes a substantial contribution to the structure of the adult head capsule. By its very form and the nature of emergence of the adult organ from its enclosing peripodial sac the antenna is brought to its new adult position on the head, and the genal area of the adult head capsule is greatly extended by additions from the antennal peripodial membrane. Further examples of imaginal development in the larva providing for the adult head capsule are found in the labrum and clypeus and possibly in the labium. The clypeal development is the more interesting, since by growth of a hypodermal imaginal rudiment there is formed a deep clypeal fold out of which there comes into existence the pupal crest. This in turn provides for the larger clypeus of the adult, to the inner wall of which are attached most of the dorsal dilator muscles of the imaginal sucking pump.

We may place the development of the adult epicranium in a category by itself. It has no existence in the larva, and no special imaginal rudiment is seen in the larva in preparation for its development. Only in the pupa is the epicranium produced to complete the cranial architecture of the adult, conferring on the head a mobility which was not enjoyed by the larva.

Gonin (1894) correctly interpreted the phases in the development of the pupal crest and of the labial palp. He failed, however, to notice the peculiarities of the antennal development with the consequent changes in the form of the head capsule. He also did not throw any light on the development of the epicranium as here described.

It has been remarked that Keilin (1915) had established in Diptera Cyclorrhapha that absent larval appendages were represented by sensilla. It was also pointed out that Perez (1918) had observed a phenomenon similar in kind if not in degree in the apodous larva of *Phytonomus*. In this latter case the tip of the developing adult appendage, within its wide open peripodial sac, maintained throughout larval life a contact with the larval cuticle by way of certain sensilla. This condition is found also in *Pieris*, for in antennae, maxillae and labial palps the larval sensilla are found in similar close association with the developing adult structure within. Only at the end of larval life is this association severed by the degeneration of the larval sense cells.

The last point to which reference may be made is the steady growth, with continuous mitosis of the cells, of imaginal rudiments during instar periods. This is best seen in the labial palp, where almost the whole growth occurs in the period between the fourth and fifth moults. Measurements of the imaginal rudiments have confirmed that their growth continues between moults.

This fact is important, because during larval life mitotic activity of ordinary (not imaginal) larval cells is restricted to the moult period and does not take place in the period between one moult and the next.

Acknowledgments.

I take pleasure in thanking Professor L. E. S. Eastham, who suggested the problem, supervised my research studies and prepared this paper for the press. To Mr. Hancock, also of the Department of Zoology, Sheffield University, I owe my thanks for the care with which he prepared the photographs.

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PLATE I.

FIG. 1.—L.S., antenna early 5th instar. I.P.M., imaginal cells in peripodial membrane ; I.C., imaginal cells of antenna ; S.C., sense cells of larval antenna.

FIG. 2.—L.S., antenna late 5th instar. An., antenna ; I.P.M., imaginal cells in peripodial membrane ; D.S.C., degenerating sense cell of larval antenna.

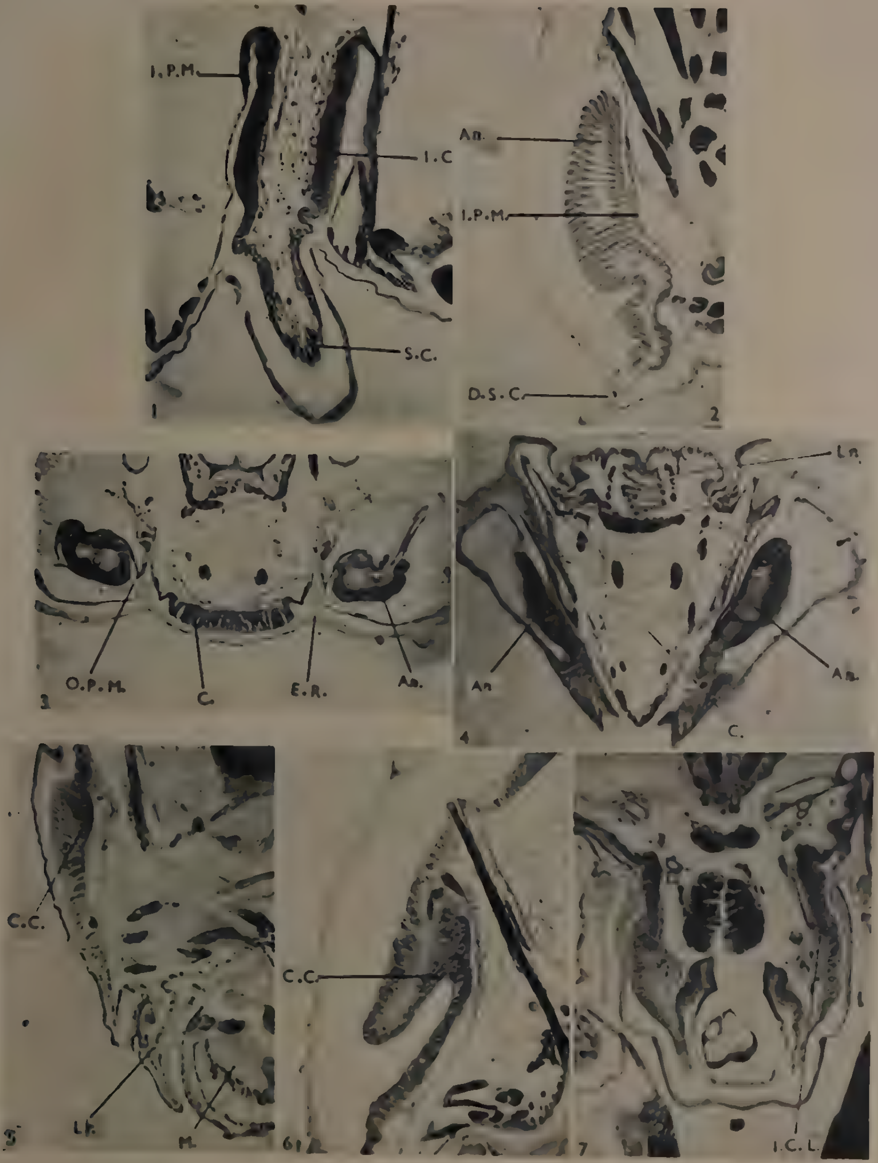
FIG. 3.—T.S., through head early 4th instar. An., antenna ; C., clypeus with imaginal cells developing ; E.R., epistomal ridge of larval head ; O.P.M., opening of antennal peripodial sac.

FIG. 4.—Frontal section through clypeus, C, of 5th instar showing antennal rudiment An., lying along the epistomal ridge. Lr., Labrum.

FIG. 5.—L.S., larval head early 5th instar showing rudiment of clypeal crest, C.C. ; labrum Lr. ; mandible, M.

FIG. 6.—L.S., Larval head late 5th instar, showing clypeal crest, C.C.

FIG. 7.—Horizontal section larval labium late 5th instar showing imaginal cells of labial palp, I.C.L.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The development of imaginal buds in the head of *Pieris brassicae* L.

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THE CLASSIFICATION OF THE DRYINIDAE (HYM.), WITH DESCRIPTIONS OF NEW SPECIES.

By O. W. Richards, M.A., D.Sc., F.R.E.S.

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With 11 Text-figures.

During a recent examination of material belonging to this family, it was noticed that the number of tibial spurs varies, and can be used in conjunction with other characters to define three well-marked subfamilies within the Dryinidae, as follows:

Females.

1. Fore trochanter usually not or hardly longer than broad, rarely twice as long as broad. Tibial spurs 1, 1, 1, very rarely 1, 1, 2. Occipital keel complete. Posterior angles of pronotum produced into distinct lobes. Species usually fully winged . . . . Subfamily **Anteoninae**
–. Fore trochanter more than twice as long as broad, often very elongate.
2. Tibial spurs 1, 0, 1, very rarely 1, 0, 2. Occipital keel usually absent, sometimes indicated behind the ocelli in winged forms, but most species are wingless. Posterior angles of pronotum rounded, not produced into lobes (fig. 1). Postscutellum very reduced in winged forms Subfamily **Gonatopodinae**
–. Tibial spurs 1, 1, 2, apparently very rarely 1, 1, 1. Occipital keel more or less distinct, at least dorsally. Posterior angles of pronotum produced into distinct lobes, directed towards the tegulae (fig. 2). Species fully winged, postscutellum normal . . . . . Subfamily **Dryininae**

The males are still too little known to be put satisfactorily into subfamilies. A preliminary attempt was made earlier (Richards, 1939 : 190). In all the males the tibial spurs seem to be 1, 1, 2.

In my 1939 paper I made a group Bocchini for *Bocchus* Ashmead and a few probably allied genera. At the present moment it seems more practical to merge them in the Anteoninae, at least until they have been more studied.

I have prepared below an alphabetical list of the genera of Dryinidae, together with their assignment to the three subfamilies defined above. Some genera are still of uncertain position. This applies especially to those described by Kieffer. Recent study of the types of species on which some of his genera were based shows that it is hazardous to accept his diagnoses at their face value. I believe it will be better to ignore many of his genera until their type species have been redescribed.

In the list below the three subfamilies are indicated by their initial letters and (?) implies that the position of the genus is uncertain. Any new synonymy is substantiated later.

Agonatopoides Perkins, 1907, G.
Agonatopus Perkins, 1907, G.
Allanteon Kieffer, 1914 = *Anteon* Jur.
Allodryinus Kieffer, 1922, ? D.
Allogonatopus Haupt, 1938 = *Neogonatopus* Perk.
Anteon Jurine, 1807, A.
Anteonella Dodd, 1913, ?.
Apterodryinus Perkins, 1907, G.
Bocchus Ashmead, 1893, A.
Campylonyx Westwood, 1835, ? A.
Chalcogonatopus Perkins, 1905, G.
Chelogynus Haliday, 1838 = *Anteon* Jur.
Chelothelius Reinhard, 1863, A.
Chlorodryinus Perkins, 1905, D.
Ctenodryinus Arlé, 1935 = *Neodryinus* Perk.
Cyrtogonatopus Kieffer, 1907, ? G.
Deinodryinus Perkins, 1907, A.
Dicondylus Haliday *in* Curtis, 1829–30, G.
Digonatopus Kieffer, 1913, G.
Donisthorpina Richards, 1939, G.
Dryinus Latreille, 1804, D.
Echthrodelphax Perkins, 1903, G.
Epigonatopoides Richards, 1939, G.
Epigonatopus Perkins, 1905, G.
Eucamptonyx Perkins, 1907, G.
Eugonatopus Perkins, 1905 = *Chalcogonatopus* Perk.
Eukoebeleia Perkins, 1905 = *Bocchus* Ashmead.
Gonatopus Ljungh, 1810, G.
Gynochelys Brues, 1906, A.
Haplogonatopus Perkins, 1905, G.
Hesperodryinus Perkins, 1907, A.
Laberinus Ogloblin, 1932, ? G.
Laberius Kieffer, 1914 = *Dicondylus* Hal. *in* Curt.
Lasianteon Kieffer, 1913 ? = *Anteon* Jur.
Lestodryinus Kieffer, 1911 = *Dryinus* Latr.
Liodryinus Kieffer, 1906 = *Anteon* Jur.
Lonchodryinus Kieffer, 1905, ?
Mercetia Kieffer, 1906, G.
Mesodryinus Kieffer, 1906, D.
Metagonatopus Ogloblin, 1932, G.
Monogonatopus Richards, 1939, G.
Mystrophorus Förster, 1856, A.
Neoanteon Fouts, 1922, A.
Neochelogynus Perkins, 1905 = *Anteon* Jur.
Neodryinus Perkins, 1905, G.
Neogonatopus Perkins, 1905, G.
Pachygonatopus Perkins, 1905, G.
Paradryinus Perkins, 1905, D.
Paragonatopus Perkins, 1905, G.
Paranteon Perkins, 1905, A
Perodryinus Perkins, 1907, D.
Phanerodryinus Roepke, 1916 = *Neodryinus* Perk.
Phorbasia Kieffer, 1914 = *Bocchus* Ashmead.
Plastodryinus Kieffer, 1906, ?
Platygonatopus Kieffer, 1906, G.
Plectrogonatopus Richards, 1939, G.
Prenanteon Kieffer, 1913, A.
Pristogonatopus Kieffer, 1913, ? G.
Prodryinus Kieffer, 1906 = *Neodryinus* Perk.
Prosanteon Perkins, 1905 = *Anteon* Jur.
Pseudogonatopus Perkins, 1905, G.
Psilanteon Kieffer, 1913 = *Prenanteon* Kieffer.
Psilodryinus Kieffer, 1906 = *Neodryinus* Perk.
Tetradryinus Kieffer, 1906, ?
Tetrodontochelys Richards, 1939, G.
Thaumatodryinus Perkins, 1905, D.
Trichogonatopus Kieffer, 1909, ?
Trichogonatopus Hellén, 1930 (*nec* Kieffer), G
Tridryinus Kieffer, 1913, ?
Trigonatopus Kieffer, 1913, ? G
Trisanteon, Kieffer, 1913, A.
Xenanteon Kieffer, 1913 = *Anteon*, Jur.

SUBFAMILY ANTEONINAE.

If the group allied to *Bocchus* Ashmead be included, the well-established genera can be separated as follows. Genera known only from their descriptions are marked with an asterisk.

1. Mandibles tridentate. Eyes distinctly hairy. Enlarged claw serrate beneath. Tibial spurs 1, 1, 1. Winged or brachypterous. Gaster subpetiolate . . . . **Bocchus** Ashmead

–. Mandibles quadridentate, dorsal tooth sometimes small (*Mystrophorus* Först.). Eyes not or very feebly hairy . . . . 2.

2. Fully winged species . . . . 3.

–. Brachypterous to nearly apterous species. Gaster sessile . . . . 10.

3. Gaster distinctly petiolate . . . . **Neoanteon** Fouts*

–. Gaster subsessile. . . . . 4.

4. Tibial spurs 1, 1, 2. First segment of gaster more than twice as long as broad. Pterostigma somewhat narrow, elongate-ovate, radial vein long, angled. Propodeum nearly smooth, not areolate nor reticulate **Deinodryinus** Perkins

–. Tibial spurs usually 1, 1, 1. First segment of gaster not more than twice as long as broad. Propodeum usually reticulate and areolate . . 5.

5. Enlarged claw of fore tarsus with lamellae, or somewhat serrate and with bristles. Pterostigma long and narrow, radius hardly angled. Pronotum more than twice as long as broad, posteriorly markedly constricted. Notaulices indicated but weak. Clypeus bidentate **Hesperodryinus** Perkins

–. Enlarged claw of fore tarsus simple. Pterostigma shorter, subtruncate. Pronotum usually much shorter and never so strongly constricted posteriorly. Clypeus ventrally rounded . . . . 6.

6. Fore trochanter somewhat elongate, one and a half times as long as broad. Notaulices absent. Radial vein somewhat angled, wings banded . . . . **Chelothelius** Reinhard*

–. Fore trochanter short and globular. Notaulices indicated, at least in front. Wings not banded, at most with a slight distal cloud . . 7.

7. Notaulices deep and complete. Mesopleuron with a strong anterior vertical and an obliquely transverse furrow, both strongly crenate. Pronotum also with transverse and postero-lateral crenate furrows. Two parts of radius of equal length, slightly angled . **Trisanteon** Kieffer

–. Notaulices incomplete. These various furrows if present in part, shallower and not so strongly crenate. . . . . 8.

8. Distal part of radial vein more or less distinctly shorter than proximal part, the two parts forming a more or less distinct angle. Antennae somewhat clavate in female, segments shorter in both sexes **Anteon** Jurine

–. Parts of radial vein of about equal length and together forming a curve rather than an angle. Antennal segments longer and in female not distally thickened . . . . 9.

9. Female (male not seen) with frons and vertex convex between the eyes (more as in male **Anteon**). Antennal segments 8–9 three times as long as broad. Fore tarsus short; chela hardly longer than segment 1; enlarged claw stout, strongly curved. Posterior surface of propodeum mainly smooth . . . . **Paranteon** Perkins

–. Frons and vertex flat between eyes. Antennal segments 3–6 much longer, 8–9 rather shorter, at least in female. Fore tarsus with segment 1 longer but chela longer still. Propodeum reticulate and partly areolate . . . . **Prenanteon** Kieffer

10. Female. Tibial spurs 1, 1, 2, the second one of hind tibia short. Tip of chela strongly sinuate. Wings greatly reduced. Antennae weakly clavate, segments 8–9 about three times as long as broad **Gynochelys** Brues

–. Tibial spurs 1, 1, 1 . . . . 11.

11. Antennal segments elongate, distal ones not thickened **Prenanteon** Kieffer
–. Antennal segments shorter and in female distally thickened . . . 12.
12. Mandibles quadridentate . . . . **Anteon** Jurine
–. Mandibles tridentate with a slight indication of a fourth tooth **Mystrophorus** Förster

Liodrynus Kieffer, 1913, monobasic for *Anteon doddi* Kieffer, 1911 = *Anteon* Jurine **syn. n.** The pronotum is a little broader than long. Fore tarsus with segment 4 hardly longer than 1, 2 with a very strong anterior hook, 5 with four or five rows of fine lamellae along its whole length and a denser group at the end. It would form a species group somewhat different from the subgenus *Chelogynus* Hal. *in* Curt.

The genus *Hesperodryinus* Perk. has not previously been put into this group and its general appearance is of a Dryinine. But in the type species, *H. amphiscepae* Perk. ♀, the fore trochanters are globular, the tibial spurs are 1, 1, 1, the occipital keel is nearly complete and the malar space is crossed by a strong furrow. All these characters ally it to the present subfamily, although the venation, bidentate clypeus and general appearance agree with the Dryininae.

I have not examined *Chelothelius* Reinhard, but Mons. L. Berland tells me that the fore trochanters, though strongly swollen, are distinctly longer than broad. The tibial spurs are difficult to see, but are 1, 1, 2 (*C. gryps* Reinh.) and 1, 2, 1 or 1, 2, 2 (*C. berlandi* Bernard).

Campylonyx Westw. has not been re-examined since its description and the unique type specimen does not seem to be traceable ; it should be in the Dejean collection. The brief description somewhat suggests the present group, rather than the Dryininae where it has usually been placed. It is said to be recognizable by having two longitudinal keels on the propodeum but may really be the same as *Anteon* subg. *Chelogynus*. In this last group Ceballos (1927 : 108, fig. 5) has figured an extremely brachypterous specimen.

SUBFAMILY DRYININAE.

Kieffer placed all winged genera which were not Anteonines in the present group. Perkins has already shown that *Echthrodelphax* Perk. was allied to the Gonatopinae. It now appears that *Neodryinus* Perk. and *Mercetia* Kieff. have a reduced postscutellum, no posterior lobes to the pronotum and no spur to the mid tibia ; they should, therefore, also be transferred to the Gonatopinae. The following genera of which the type species was described by Kieffer seem to be of so uncertain a status as to be left on one side : *Allodryinus* Kieff., *Lonchodryinus* Kieff., *Plastodryinus* Kieff., *Tetradryinus* Kieff., and *Tridryinus* Kieff. Judging by Kieffer types which I have recently examined, these genera may well be found to have quite different characters from those which Kieffer ascribed to them, or else to be synonyms of other genera. Probably there are a number more genera to be recognized, but it will need a great deal more study to sort them out. Meanwhile, the following key will separate the females of the seven well established genera. By no means all of the species which have been placed in them have been done so correctly.

1. Enlarged claw of fore tarsus more than three times as long as the tibia, with a long row of spines. Mesoscutum without notaulices. Lobes of pronotum well separated from the tegulae . . **Megadryinus** gen. n.

–. Enlarged claw of fore tarsus shorter than the tibia . . . . 2.
2. Antennae longer than the body, third segment not much longer than or even shorter than the fourth. Pronotal lobes reaching the tegulae **Thaumatodryinus** Perkins
–. Antennae shorter, segment 3 much longer than 4. Pronotal lobes not reaching the tegulae . . . . 3.
3. Enlarged claw of the fore tarsus simple, without lamellae. Mesoscutum without notaulices. Pronotum not markedly humped, without transverse impressions . . . . **Perodryinus** Perkins*
–. Enlarged claw of fore tarsus with lamellae . . . . 4.
4. Mesoscutum without a trace of notaulices . . . . **Mesodryinus** Kieffer
–. Notaulices more or less strongly developed . . . . 5.
5. Occipital margin only indicated centrally. Pronotum not humped, notaulices distinct but not quite complete. Colours pale **Chlorodryinus** Perkins
–. Occipital margin complete. Pronotum more or less strongly humped and transversely impressed . . . . 6.
6. Pronotum with two transverse impressions. Notaulices rather weak, not easily seen amongst the pronounced longitudinal sculpture of the mesoscutum. Head not concave . . . . . **Paradryinus** Perkins
–. Notaulices complete. Vertex somewhat concave . . . **Dryinus** Latreille

Megadryinus gen. n.

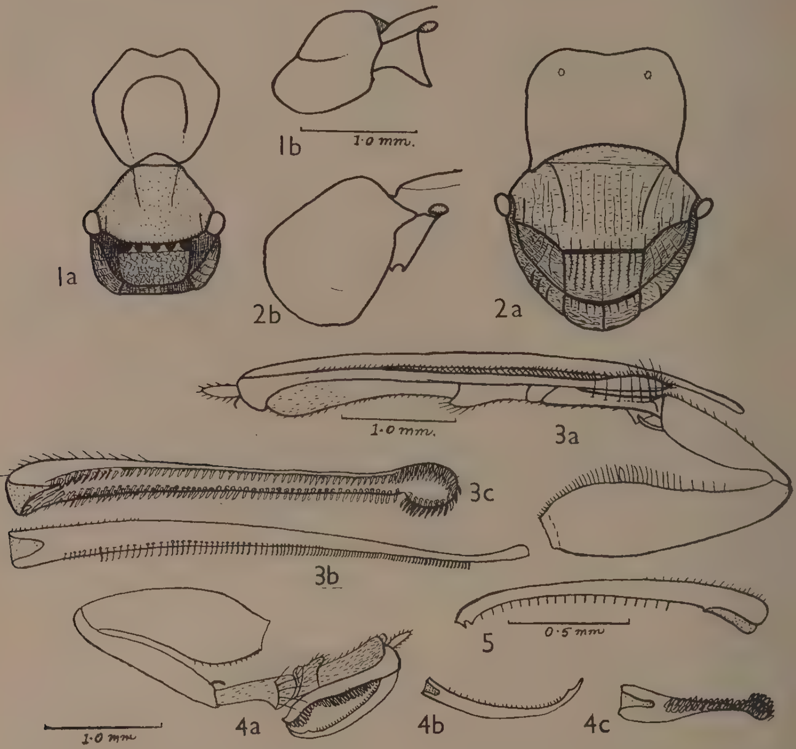
Chela immensely large, claw more than three times as long as fore tibia ; tarsi also very long, segment 4 as long as tibia, segment 5 with two distinct rows of lamellae ; claw with a row of slightly hooked spines and with its end simple in one view, slightly spatulate in the other. Antennae as long as head + thorax ; segment 3 three times as long as segments 4 + 5. Vertex slightly transversely concave. Pronotum convex but without a transverse impression except right at hind margin ; lateral lobes strong but not reaching tegulae. Mesoscutum without notaulices or parapsidal furrows.

Type of genus = *Megadryinus magnificus* sp. n.

Megadryinus magnificus sp. n.

♀. Black ; mandibles, clypeus, part of malar area adjacent to it, antennae 1–2 and very small proximal part of 3, tips of fore coxa and trochanter, fore femur and tibia, deep reddish. Antennae 6–10, distal part of both pieces of chela, brown. Proximal third of enlarged fore claw whitish. Wings hyaline with a dark band, not quite reaching hind margin, at level of pterostigma and a discal dark spot near base. Base of pterostigma pale, veins dark. Tibial spurs pale. Length about 11·0 mm. Length of fore wing 6·5 mm.

Head with eyes in dorsal view three times as broad as long, posteriorly shallowly emarginate. Malar space crossed by a distinct keel. Mandibles with four teeth, ventral one only twice as large as next one. Clypeus rounded triangular, somewhat less than twice as broad as long, ventrally shallowly emarginate. Vertex a little shining, duller below, with moderately strong, irregular rugae ; scrobes with dense silvery pubescence, pubescence elsewhere sparser and more erect, surface shallowly transversely concave ; occipital keel strong and especially prominent where it turns round on to the ventral surface. Ocelli in a broad isosceles triangle, hind pair separated by half their diameter from the keel, POL : OOL = 3 : 5. Antennae about as long as head and thorax, slightly thickened from segment 4 onwards ; segment 1 curved, four times as long as broad, 2 a little longer than broad, segment 3 as long as width of head with eyes, four times as long as segment 1 and about three times as long as 4 + 5, segment 4 about five times as long as broad, 5–9 progressively shorter, 9 twice as long as broad, 10 as long as 6. Maxillary palp extending back to hind margin of proepisternum. Pronotum about one and one-third times as long as broad, anterior margin just concave; front margin of pronotum very faintly emarginate, hind margin with a slight upturned border, not emarginate; profile convex and sinking to a rugose cross-furrow before posterior margin, small callosities on each side just behind anterior margin, surface finely cross-striate with silvery pubescence except at sides in front, where it is smooth and shining; posterior lobes well separated from the tegulae. Mesoscutum twice as broad as long, very little convex, without parapsidal furrows or notaulices; scutellum flat, not quite twice as broad as long, separated from scutum by a deep, narrow furrow, surface like that of scutum, a little shining with a network of coarse rugae and rather sparse silvery pubescence; postscutellum half as long as scutellum, rather more coarsely sculptured; mesopleuron with irregular rugae, rather dull, sculpture finer on prepectus and on a small area near the mesepisternal scrobe. Metapleuron shining with regular



Figs. 1–5.—(1) *Neodryinus lawanae* sp. n. ♀. *a*. Thorax in dorsal view. *b*. Pronotum and anterior part of mesothorax, from the left. (2) The same, in *Mesodryinus poecilopterae* Rich. ♀. (3) *Megadryinus magnificus* sp. n. ♀. *a*. Posterior view of left fore leg. *b*. Enlarged claw, seen from inside. *c*. Fifth tarsal segment, seen from inside. (4) *Mesodryinus poecilopterae* Rich. ♀. *a*. Posterior view of left fore leg. *b*. Enlarged claw. *c*. Fifth tarsal segment, seen from inside. (5) *Mesodryinus ruficauda* sp. n. ♀. Enlarged claw.

longitudinal keels. Propodeum with dorsal area longer than mesoscutum, somewhat posteriorly truncate, angles rounded right angles, surface shining with radiating longitudinal keels and smaller transverse ones; sides and posterior surface strongly reticulate-rugose; latter with rather strong converging lateral keels, spiracle elongate, transverse. Tibial spurs 1, 1, 2. Fore coxa (fig. 3*a*) two and a half times as long as broad, with dense, partly outstanding pubescence; trochanter three-quarters as long as tibia, very strongly and suddenly clavate in distal third; fore femur moderately thickened, distal stalk short, length equal to six times its greatest width, ventrally with rather close outstanding pubescence; fore tibia not quite as long as tarsal segments 1–3, much thickened towards apex, greatest thickness half that of femur; fore tarsi with segment 1 seven times as long as broad in middle, just after base with a short oblique keel from which a row of long bristles arises; segment 2 quadrate; segment 3 considerably widened, with dense appressed ventral pubescence, about three times as long as broad, neither 2 nor 3 hooked; segment 4 as long as tibia, somewhat widened distally, at least ten times as long as broad with a dense ventral row of long bristles; segment 5 (fig. 3*c*) with articulating part short, about quadrate, chelate part very long, extending to base of first tarsal segment, inner surface shining with a dense row of short white lamellae along each edge, and round the circular apical expansion; enlarged claw (fig. 3*b*) extending by the length of tarsal segment 3 beyond the chelate portion of segment 5, in one view attenuate to the apex and in the other attenuate but somewhat spatulate at apex; no subapical tooth; inner surface with row of about 90 short white bristles, not quite reaching either end. Mid and hind femora with conspicuous outstanding pubescence beneath. Hind femur moderately clavate, distal stalk one-fourth its length. Fore wing with pterostigma about four times as long as broad, pointed but moderately broad, radius weakly angled, distal part a little longer than proximal. Gaster smooth and shining.

Male unknown.

Type ♀, B.W.I.: Trinidad, Arima, 22.viii.1921 (*A. Busck*) (bred) (U.S.N.M.). Paratypes: St. Augustine, vi.1949, ♀ bred *Ormenis* sp. on Cacao (*F. J. Simmonds*); Diego Martin, 28.vi.1945, ♀ (*E. McC. Callan*) (my collection).

Cocoon a flattened oval dome on leaf, 13 × 10 mm., about 3 mm. high, almost transparent, exit hole near one end.

The specific name is due to Dr. S. A. Rohwer, who, however, did not publish a description of the species. I am indebted to Mr. K. V. Krombein for the loan of two of the specimens from the collection of the U.S. National Museum. The paratype from St. Augustine will be placed in the British Museum.

Mesodryinus Kieffer.

I am indebted to Dr. Delfa Guiglia for the loan of the holotype female of *Dryinus niger* Kieffer, 1904, the species on which this genus was based. It turns out to be the same as *Mesodryinus brittanicus* Richards, 1939; the British specimens have the hind femora and tibia rather more extensively dark and the sculpture of the mesoscutum rather finer, with less tendency to be longitudinal. More material would be required to decide whether these difference have any significance.

Mesodryinus niger (Kieffer).

Dryinus niger Kieffer, 1904. Italy, Vallo Lucania, Solari, v.1902.
Mesodryinus brittanicus Richards, 1939: 228, figs. 42, 43. Dorset. **syn. n.**
M. brittanicus Richards, 1948. Northants.

Redescription of the holotype.

♀. Black; palpi, mandibles, clypeus, antennae, legs except proximal two-thirds of hind coxa, distal half of hind femur and tibia which are black and all tarsi which are creamy, reddish-brown. Tegulae dark brown. Wings hyaline, fore wing with two ill-defined dark bands; venation brown, bases of long veins and of pterostigma whitish; length 3·5 mm., length of fore wing 2·7 mm.

Head and thorax dull with short silvery pubescence, which is denser on face, sides of thorax and posterior surface of propodeum. Gaster smooth and shining. Head with eyes, in dorsal view, a little more than twice as wide as broad, posteriorly regularly and somewhat deeply emarginate. Clypeus feebly sculptured, not quite semicircular, centre of ventral margin hardly perceptibly excised. Malar space with a short, posteriorly incomplete furrow. Mandibles with a strong transverse impression just after articulation, then strongly convex, at distal end ventral tooth very long and acute, four times as long as its proximal breadth; next tooth also long and acute, rather more than half as long; two dorsal teeth very small. Frons and vertex finely alutaceous, sculpture tending to form very fine longitudinal lines; scrobes obsolete, vertex flat and on a level with eyes; posterior margin very weak, only visible for a stretch behind ocelli, which are in a somewhat broader than equilateral triangle, touching the margin, POL : OOL = 4 : 5. Antennae extending back to about brow of propodeum, slightly thickened from segment 4 onwards; segment 1 curved, twice as long as broad, 2 ovate, a little longer than broad, 3 not quite as long as distance between eyes on vertex, three and a half times as long as 1, a little longer than 4 + 5, about eight times as long as broad, 4 five times as long as broad, 4–9 progressively a little shorter, 9 two and a half times as long as broad, 10 as long as 7. Maxillary palp reaching back to about centre of proepisternum; palpi probably with 6 and 3 segments respectively. Pronotum about as long as broad, with anterior margin hardly emarginate; posterior margin very narrowly lamellate, not emarginate, dorsally finely rugose, with one or two striae on each side near posterior margin, sides finely alutaceous, latero-ventral margin smooth and transparent, in side view only slightly convex, no transverse impression; posterior lobes separated from tegula by length of latter. Mesoscutum a little more than twice as wide as long, finely irregularly rugose, with some short longitudinal rugae in front of scutellum, notaulices and parapsidal furrows absent; scutellum flat, separated by a deep, narrow furrow, more than half as long as scutum and a little more shining; postscutellum flat, not quite half as long as scutellum, similarly sculptured; propodeum with dorsal area flat, posterior angles rounded right-angles, surface almost on same level as postscutellum with irregular raised rugae, stronger and forming a much larger mesh than on mesoscutum; spiracle small but elongate, sides finely rugose, posterior surface without lateral keels, sculpture almost resembling large, shallow, confluent punctures. Mesopleuron finely rugose, metapleuron anteriorly smooth and shining, posteriorly with fine transverse striae. Tibial spurs 1, 1, 2. Fore coxa not visible; fore trochanter apparently little clavate; fore femur shining with sparse, fine pubescence, strongly thickened, length equal to three and half times its greatest width; fore tibia three-quarters as long as tarsi, moderately thickened, two-fifths as wide as greatest width of femur, fore tarsi with segment 1 four and a half times as long as broad in middle, cylindrical, a little thickened at apex, where there are some outstanding bristles, segment 2 transverse, a little hooked in front with 2–3 long bristles, segment 3 about twice as long as broad, also a little hooked in front at anterior end, segment 4 about two and a half times as long as broad, about two-thirds as long as 1, articulating part of segment 5 about quadrate, chelate part extending back to proximal end of 3, slightly and regularly curved, end little expanded, lamellae small and fine, forming a dense ring round end but extending only a short distance towards articulation; enlarged claw slightly curved, apex rather blunt, without subapical tooth, with a row of bristle-like lamellae towards apex. Mid and hind legs moderately shining, very finely pubescent, hind femur strongly thickened, distal quarter forming a stalk. Pterostigma three times as long as broad.

It was difficult to recognize this species from Kieffer's description since he states that the pronotum is shorter than the head and hardly as long as the mesoscutum, which is far from true. The type is gummed firmly down flat, with most of the venter hidden.

Mesodryinus poecilopterae Richards, 1947.

This species was described from Trinidad where Dr. E. McC. Callan bred it from the Flatid *Poeciloptera phalaenoides* (L.); four females and one damaged male were available. I have now received a series of both sexes from the collection of the U.S. National Museum, kindly sent by Mr. K. V. Krombein. The original description may be amended as follows:

Female.—Clypeus shallowly emarginate; antennal segment 3 only three-quarters as long as width of head with eyes, three and a half times as long as segment 1, and two and a half times as long as 4 + 5. Malar space crossed by a distinct keel. Mandibles with four teeth, ventral one not more than twice as long as next one. Maxillary palpi extending back to centre of proepisternum. Pronotum with anterior margin very feebly excised, posterior margin narrowly laminate, not emarginate. Pubescence everywhere short and sparse, including on legs. Tibial spurs 1, 1, 2. Fore trochanter (fig. 4*a*) only gradually clavate; fore femur very much thickened, length equal to four times its greatest width; fore tibia not much clavate, less then half as wide as femur; segment 4 of fore tarsi with a row of long ventral bristles on proximal half, segment 5 (fig. 4*c*) with lamellae in one double row, not separated into two rows along the edges, enlarged claw (fig. 4*b*) with 22–25 bristle-like lamellae.

Male.—Mid coxa and base of gaster more or less brown. Fore wing with a slight cloud opposite the pterostigma. Length 4·7 mm., length of fore wing 3·3 mm.

Antennae a little longer than head + thorax + propodeum, a little attenuate at apex; segment 1 twice as long as broad, 2 a little longer than broad, 3 about eight times as long as broad, almost as long as least distance between eyes, one and two-thirds times as long as 1 + 2, as long as 4 + 5, 4–9 becoming gradually a very little shorter, 9 three and a half times as long as broad, 10 as long as 6. Metapleuron strongly depressed, smooth, with weak longitudinal striae. Posterior and ventral part of mesopleuron more finely sculptured than rest of thorax, duller, fine striae tending to run vertically and interspersed with some punctures. Tibial spurs 1, 1, 2. Pubescence shorter than female. Abdominal sternite 9 (fig. 6*b*) with a short anterior stalk, posteriorly acutely triangular but without bristles. Genitalia (fig. 6*a*) with penis valves forming rounded hooks, digitus with one small serration but no apical bristle, volsella plate with four bristles, paramere with no long process from its anterior end.

Additional specimens examined: REP. SALVADOR: San Salvador, 7.iii.1925 ex *Poeciloptera vulgaris* var. *completa* Jac., 3 ♀ (*K. A. Salman*); same data, 6.iii.1925, 3 ♂, 2 ♀. The male cocoons are somewhat smaller than those of the female, about 6·5 × 4·5 mm.

Mesodryinus ruficauda sp. n.

♀. Black; clypeus, mandibles, antennae, fore legs (except enlarged claw), suffusion of femur, tip of tibia and most of tarsus of mid legs, suffusion of tibia and most of tarsus of hind legs, gaster segments 5–7, bright reddish brown. Enlarged claw whitish brown. Tegula pitchy red. Wings hyaline with a dark band, sharply defined inwardly, at centre of pterostigma, not crossing vein CU_1, discal dark spot towards base; venation dark, bases of long veins and proximal third of pterostigma whitish. Length about 6·0 mm., length of fore wing 4·2 mm.

Differs from *M. poecilopterae* Rich. as follows : Antennae damaged but segments apparently with the same proportions ; pronotum a little duller, fine striations a little stronger, anterior margin narrowly lamellate, more widely emarginate ; mesoscutum a little more transverse ; fore femur somewhat less thickened ; fore tarsus with segment 5 considerably longer, spatulate end a little hooked where it abuts on basal tarsal segments ; lamellae smaller and on spatulate end less numerous, enlarged claw (fig. 5) longer, end truncate and forming a small hook ; subapical tooth almost contiguous with hook, inner surface with 20 fine bristle-like lamellae.

Type ♀, COSTA RICA : San Pedro de Montes de Oca, 3.iii.1933, ex cocoon on leaf (*C. H. Ballou*) (U.S. Nat. Mus.). Cocoon perfectly transparent, flatter and more circular than in *M. poecilopterae*, 8·5 × 7·0 × 2·0 mm.

Dryinus Latreille, 1894.

This genus, judging by the few species which I have seen, may well be composite. *D. pyrillae* (Kieffer) seems to have tibial spurs 1, 1, 1, yet on other characters it clearly belongs to this subfamily.

SUBFAMILY GONATOPODINAE.

The majority of the females of this group are completely apterous and *Gonatopus*-like. These forms are largely classified according to the number of palpal segments and are not considered here.

Apterodryinus Perkins, in spite of Dr. Perkins's opinion and of the view which I expressed (1939 : 189), seems to be best placed here since the tibial spurs are 1, 0, 1.

The winged members of the subfamily are :

(a) *Echthrodelphax* Perk. The position of this genus was correctly recognized by Dr. Perkins, but Kieffer transferred it to the Dryininae. It has tibial spurs 1, 0, 1, postscutellum very short, the pterostigma very narrow, and the pronotum not produced into posterior lobes.

It is recognized by the converging notaulices which meet at the posterior margin of the mesoscutum ; and by the palps, which have 4 maxillary and 2 labial segments.

(b) *Mercetia* Kieff.—From the figure given by Ceballos (1927 : 100, fig. 1), it appeared that this genus belonged here. Dr. Ceballos was kind enough to send me specimens of *M. longicollis* Kieff. (Ceballos det.) and of *M. betica* Ceb. and *M. obscura* Ceb. The tibial spurs are 1, 0, 1 or (*obscura*) 1, 0, 2. The pronotum has no posterior lobes and the postscutellum is very short. The palpi have not been properly described.

It is recognized by the long, complete notaulices, which though rather close are quite separate to the posterior margin of the mesoscutum.

(c) *Neodryinus* Perk.—This genus has been studied in some detail and two of Kieffer's genera have been found by the study of the holotypes of the type species to be synonyms of it.

Neodryinus Perkins, 1905.

Type of the genus = *N. koebelei* Perkins, 1905, by original designation.

Prodryinus Kieffer, 1906. **syn. n.**

Type of the genus = *Dryinus brachycerus* Kieffer, 1904, by original designation.

The type species is redescribed below. The genus may be used in a subgeneric sense for the species (principally American) of *Neodryinus* with an unarmed chelar claw.

Psilodryinus Kieffer, 1906. **syn. n.**

Type of the genus (originally a subgenus of *Neodryinus*) = *Dryinus acuticollis* Kieffer, 1905.

The type species is redescribed below. The genus is a synonym of *Neodryinus* subgen. *Prodryinus* Kieff., that name having priority on the page (Kieffer, 1906 : 497).

Phanerodryinus Roepke, 1916. **syn. n.**

Type of the genus = *Phanerodryinus javanus* Roepke, 1916 (*see below*).

Ctenodryinus Arlé, 1935. **syn. n.**

Type of the genus = *Prodryinus* (*Ctenodryinus*) *affinis* Arlé, 1935 (the only species originally included).

Neodryinus brachycerus (Kieffer, 1904).

♀. Black; mandibles pitchy with white discal patch; antennae brown with scape white and 4–10 darker than 2–3; palpi dark brown; fore legs with articulations, distal third of femur especially above, tibia and tarsi, brown; mid and hind legs with distal part of femur and centre of tibia brown suffused, tarsi creamy with last segment blackish. Tegula pitchy. Fore wing hyaline with two rather well-defined brown bands, area between them (including proximal half of pterostigma) somewhat milky. Veins brown, base of costa and Sc + R white. Length 3·3 mm., length of fore wing 2·2 mm.

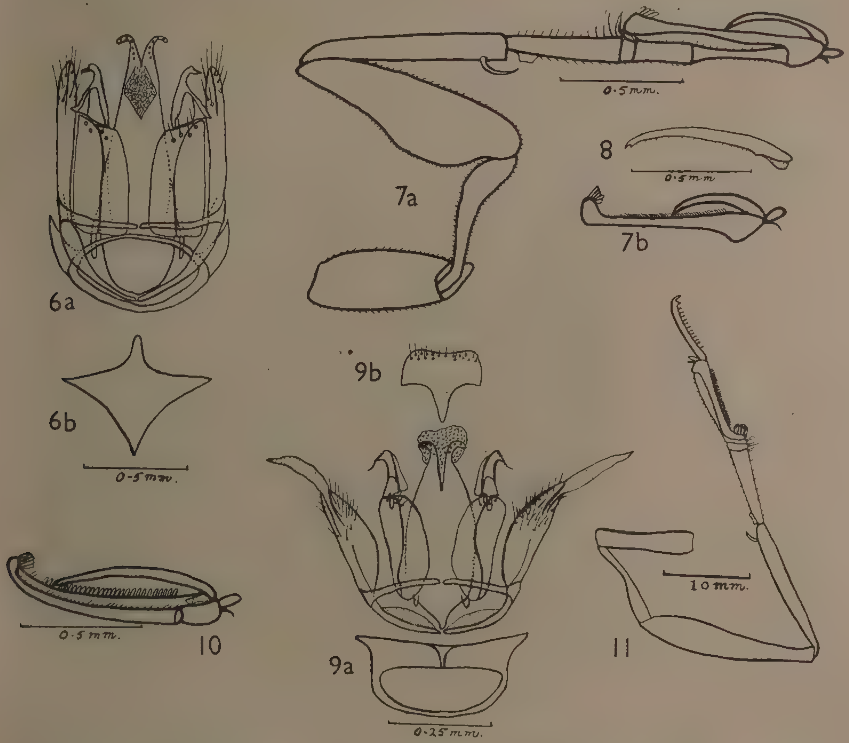
Body dull, finely rugose, with very short, sparse inconspicuous pubescence. Gaster smooth and shining. Head with eyes, in dorsal view, two and a half times as broad as long, posteriorly shallow emarginate over central half. Clypeus almost circular, ventral margin not emarginate, surface finely granulate. No keel or furrow on malar space. Mandibles with four teeth, ventral one somewhat more than twice as long as next one, but not unusually long, two dorsal ones very small but distinct. Frons and vertex very finely rugose, vertex flat, very little depressed below level of eyes, posterior margin very weak and only visible on central half. Ocelli in an equilateral triangle touching the margin, POL : OOL = 1 : 3. Antennae extending back to posterior margin of scutellum, slightly thickened from the end of segment 4, segment 1 little curved, three times as long as broad, 2 twice as long as broad, narrow, 3 three-quarters as long as distance between eyes, two and a half times as long as 1, one and a half times as long as 4 + 5, eight times as long as broad, 4 four times as long as broad, 4–7 progressively a little shorter, 7 = 8 = 9, twice as long as broad, 10 as long as 6. Maxillary palpi extending to the back of the head. Pronotum one-third longer than broad, considerably wider in front than behind, front margin feebly emarginate, hind margin scarcely lamellate, not emarginate, a strong transverse impression at anterior third, considerably humped behind this, surface very finely granulate, only a very narrow ventro-lateral margin smooth, postero-lateral corners completely rounded, not produced into lobes. Mesoscutum two and a half times as broad as long, surface with fine, mainly longitudinal rugae and granulate interstices, scutellum flat, two-thirds as long and similarly sculptured, separated by a narrow and rather shallow furrow; postscutellum linear, hardly visible ; propodeum with dorsal surface somewhat longer than mesoscutum + scutellum, running into posterior surface in a smooth curve, sides and angles also rounded, surface with about 16 regular longitudinal striae, sides and posterior surface irregularly rugose. Mesopleuron finely reticulately rugose. Metapleuron granulate and posteriorly transversely striate. Tibial spurs 1, 0, 1, that of hind tibia hardly longer than end breadth of tibia. Fore coxa about twice as long as broad, not much narrowed distally ; trochanter half as long again as coxa, curved, distal half strongly clavate ; femur moderately thickened, rather more than three times as long as greatest width, twice as wide as tibia, which is three-quarters as long as tarsus ; tarsus with segment 1 cylindrical, five times as long as broad, as long as the other segments together, 2 transverse, a little produced and with two long bristles anteriorly, 3 twice as long as broad, hooked anteriorly at proximal end, 4 a little longer than 3, 5 with articulating part quadrate, produced part nearly extending to hook of 3, distal end a little expanded, with a double or triple row of very fine, short, densely placed, pale lamellae ; enlarged claw strongly curved, without subapical tooth or lamellae. Hind femur strongly clavate, distal third forming a stalk. Pterostigma very narrow, at least five times as long as broad.

Type ♀, ARGENTINA : 29.i.1899 (*F. Silvestri*). Gummed down on its left side. The specimen was kindly lent to me by the Museo Civico di Storia Naturale, Genova, through Dr. Delfa Guiglia.

Dryinus acuticollis Kieffer, 1905.

Female.—Black ; mandibles, antennae (at least up to segment 3), spots at sides of clypeus, sides of pronotum postero-ventrally, sides of apex of gaster, legs (except hind coxae), reddish-brown, antennae paler, thickened part of femora darker. Tegula brown. Wings hyaline, fore wing with dark, inwardly sharply defined area extending half way across from pterostigma and a large dark basal area. Veins brown, bases of all long veins and proximal half of pterostigma, whitish. Length about 4·0 mm., length of fore wing 2·5 mm.

Body dull, finely rugose, with rather conspicuous silvery pubescence, especially on mesoscutum ; gaster smooth and shining ; legs dull, very finely and closely punctured. Head with eyes, in dorsal view, two and a half times as broad as long, posteriorly rather shallowly emarginate over the central half, occiput normally produced behind the eyes on each side. Clypeus markedly transverse, ventral margin rounded. Malar space more than half as long as scape, not crossed by a keel. Mandibles probably with four teeth, lowest one acute, about twice as long as one next to it, mandible not swollen externally near its articulation. Frons and vertex with a fine reticulation of feeble rugae. Vertex flat and on a level with the eyes, posterior margin with only faint traces of a keel behind the ocelli which are in a triangle slightly broader than equilateral, posterior pair on margin, POL : OOL = 1 : 3. Antennae broken at end of segment 3, 1 a little curved, three and a half times as long as broad, 2 ovoid, twice as long as broad, 3 twice as long as 1, about eight times as long as broad, not quite as long as width of vertex at ocelli. Maxillary palpi extending back rather behind the posterior margin of head, probably with 6 segments. Pronotum just longer than broad, considerably broader in front than behind ; front margin scarcely lamellate, with a small emargination in centre, hind margin not lamellate, not preceded by an impression, with a small angular emargination ; a strong transverse impression at anterior third, strongly humped behind this, surface finely striate especially in front of impression, a little shining ; striate on sides mainly longitudinal and on hump mainly concentric ; postero-lateral corners rounded, not produced into lobes. Mesoscutum twice as broad as long, punctate with very feeble longitudinal striae, no sign of notaulices but parapsidal furrows feebly indicated. Scutellum flat, finely granulate, separated from scutum by a wide but rather shallow furrow, crossed by four rather indistinct keels. Postscutellum linear in centre, somewhat depressed below the scutellum, about one-quarter as long. Propodeum with dorsal area passing smoothly into sides and posterior surface, with about twelve rather regular longitudinal keels, with much smaller incomplete transverse ones between them, interstices a little shining, posterior surface largely hidden, sides irregularly rugose. Mesopleuron granulate with rather strongly raised reticulate rugae. Metapleuron dull, with transverse keels. Fore coxa (fig. 7*a*) distinctly narrowed distally, two and a half times as long as broad in centre; trochanter a little longer than coxa and more than half as long as femur, strongly clavate on distal third; femur rather strongly thickened, four and half times as long as its greatest width, nearly three times as wide as tibia, which is about two-thirds as long as tarsus; tarsus with segment 1 cylindrical, with a few anterior bristles but no process before apex, five times as long as broad, 2 transverse, hooked and bearing bristles anteriorly, 3 twice as long as broad in ventral view, with a slight proximal anterior process, 4 as long as 1, articulating part of 5 (fig. 7*b*) quadrate, chelate part extending back to process of 2, inside view considerably hooked at distal end, ventrally narrow and distinctly emarginate on posterior side before the spatulate apex; a single row of dense



FIGS. 6–11.—(6) *Mesodryinus poecilopterae* Rich. ♂. *a*. Genitalia, ventral view. *b*. Ninth abdominal sternite (the shorter projection is the anterior apodeme). (7) *Neodryinus acuticollis* (Kieff.). ♀. *a*. Right leg in posterior view. *b*. Right chela. (8) *Neodryinus lawanae* sp. n. ♀. Enlarged claw. (9) *Neodryinus lawanae* sp. n. ♂. *a*. Genitalia, ventral view. *b*. Ninth abdominal sternite. (10) *Neodryinus trinitatis* Rich. ♀. Right chela. (11) *Neodryinus leptopus* sp. n. ♀. Left fore leg, posterior view. Owing to the way in which the specimen is mounted and to the presence of mould, some of the details are a little uncertain.

pale lamellae, and a compact group of somewhat darker ones at apex ; enlarged claw without lamellae or subapical tooth, rather strongly curved, not extending beyond mid-point of chelate part of 5. Tibial spurs 1, 0, 1, that on tibia 3 not much longer than distal width of tibia. Hind femur strongly clavate, stalk forming about distal third. Pterostigma narrow, at least five times as long as broad, radial vein hardly angled and not emitting a distinct coloured fold or vein.

Holotype ♀, NICARAGUA : Managua (*Solari*). Kindly lent to me from the Museo Civico di Storia Naturale, Genova, through Dr. Delfa Guiglia.

Neodryinus lawanae sp. n.

♀. Black ; mandibles pitchy ; small whitish spot on each side of clypeus ; antennae with segment 1 white beneath, articulations of segments 2 and 3, and whole of segments 8–10 and part of 7, brown to orange ; legs (including coxae) and gaster dark reddish-brown, tibiae almost black, tarsi dark brown with fifth segment almost black. Tegula pitchy. Wings hyaline, fore wing with two sharply defined brown bands, veins dark brown, base of all long veins and proximal third of pterostigma white. Length 6·0 mm., length of fore wing 4·0 mm.

Body dull, finely rugose, with sparse, short silvery pubescence ; gaster smooth and shining ; legs dull, very finely and closely punctured, with microscopic pubescence. Head with eyes, in dorsal view, fully two and a half times as broad as long, posteriorly widely but shallowly emarginate, ventral part of occiput projecting backwards somewhat on each side. Clypeus about as long as broad, ventral margin rounded. Malar space fully half as long as scape, crossed by a feeble keel. Mandibles with four teeth, two lower ones of about the same length, about twice as long as broad at base. Frons and vertex dull, finely granulate, with 6–8 fine longitudinal striae each side and a stronger one in front of median ocellus. Vertex a little depressed between eyes but mostly flat, posterior margin finely keeled across central three-quarters. Ocelli in an equilateral triangle, posterior ones touching keel, POL : OOL = 1 : 6. Antennae extending back to brow of propodeum, a little thickened from end of segment 5 but attenuate from 8 ; 1 a little curved, three times as long as broad, 2 more than twice as long as broad, narrow, 3 as long as distance between eyes at occipital margin, three and a half times as long as 1, as long as 4 + 5, about ten times as long as broad, 4 six times as long as broad, 4–9 progressively a little shorter, 9 a little more than twice as long as broad, 10 as long as 7 ; 6–9 dorsally at centre with a shining, striate, shallow oval depression. Maxillary palpi extending to back of head. Pronotum just longer than broad, considerably broader in front than behind, front margin scarcely lamellate, with a small rounded emargination, hind margin not lamellate, not preceded by an impression, with a distinct angular emargination, a strong transverse impression at anterior third, considerably humped behind this, surface finely granulate, nowhere smooth and shining, upper part of sides in front very finely longitudinally striate, postero-lateral corners a little emarginate, not at all produced into lobes. Mesoscutum one-third broader than long, sides strongly converging in front where it is half as wide as between tegulae, traces of smooth notaulices and parapsidal furrows, each extending half way across, surface granulate. Scutellum flat, rather more coarsely granulate, separated from mesoscutum by a large fovea on each side and three smaller ones in centre. Central area of postscutellum flat, on same level as scutellum, one-third as long. Propodeum with dorsal area passing smoothly into sides and only feebly truncate behind, surface with about 10–12 rather regular longitudinal keels, joined by small transverse ones to form a coarse mesh, posterior surface largely granulate with lateral keels, sides more irregularly rugose. Mesopleuron granulate and feebly irregularly rugose. Metapleuron dull, with transverse keels. Fore coxa little narrowed distally, nearly three times as long as broad ; trochanter about as long as coxa, moderately clavate on distal half ; femur not much thickened, six times as long as greatest width, less than twice as wide as tibia, which is about as long as tarsus; tarsus with segment 1 cylindrical, five times as long as broad, with bristles only at apex, 2 transverse with small anterior, bristle-bearing hook, 3 nearly twice as long as broad, with a strong anterior bristle-bearing process, 4 just longer than half 1, without bristles, articulating part of 5 quadrate, chelate part extending back to process of 3, little spatulate, here surrounded by short white lamellae which elsewhere form a single central row; enlarged claw (fig. 8) moderately curved, with an acute subapical tooth, and a row of 7–8 fine hairs. Tibial spurs 1, 0, 1, that on tibia 3 nearly twice as long as breadth of tibia. Hind femur moderately clavate, stalk forming almost distal half. Pterostigma narrow, five times as long as broad, radial vein somewhat angled and emitting a brown fold at the angle.

Male.—Black. Palpi, tips of mandibles, antennae brown, the last darker distally. Fore tibiae and tarsi reddish brown. Articulations of four hind tibiae pale, mid and hind tarsi whitish, last three segments of hind tarsi dark. Tegulae pitchy. Wings hyaline. Length about 3·0 mm. Surface somewhat dull, finely granulate, pubescence inconspicuous, gaster smooth and shining. Clypeus truncate. Ocelli in a slightly curved line, at hind margin of vertex, which is not bordered, POL : OOL = 4 : 3. Antennae with short pubescence, segment 1 about quadrate, 2 of same length but one and half times as long as broad, 3–9 decreasing very slightly in length and breadth, 4 three and a half, 9 three times as long as broad, 10 as long as 8. Mesoscutum rather finely shagreened, dull, with complete notaulices separated posteriorly by one-third the anterior width of scutellum; parapsidal furrows separated by about half their length from anterior margin, scutellum with disc shagreened with some indistinct punctures, axillae and small areas on each side of apex brightly shining; postscutellum half as long as scutellum, central area rugose along its anterior margin, posteriorly shining, lateral areas shining with a striate central depression. Propodeum with an irregular mesh of fine raised rugosities, triangular central part of dorsal surface somewhat more raised and defined by indistinct keels; lateral surface smoother and defined above by a keel. Mesopleuron finely rugose, dull. Metapleuron with episternum linear, rather shining, epimeron much widened above, where defined by a keel. Tibial spurs 1, 1, 2, basitarsus as long as other tarsal segments together. Fore wing with pterostigma four times as long as broad, acutely pointed, radialis ending on costa but last third transparent, proximal part regularly curved, not emitting a pigmented spur. Gaster strongly flattened dorsally, posterior half of tergites 1–7 with a transverse band of short, rather sparse bristles, sternite 8 (abdominal 9) (fig. 9*b*) transverse, with short anterior stalk, posterior margin slightly emarginate with about 18 short bristles. Genitalia (fig. 9*a*) with penis valves forming rounded hooks, digitus with three small serrations and an apical bristle, volsella plate with four small bristles; base of parameres with a small membranous lobe but no long process, distal end of paramere with a long membranous flap.

Type ♀, MALAYA: Kuala Lumpur, 8.iii.1938, associated with *Lawana conspersa* (Walk.) (Flatidae) (*G. H. Corbett*). Allotype ♂ and 1 ♂, 2 ♀ paratypes with the same data, all in coll. B.M.

Although it seems almost certain that these males belong to the females, the genitalia are surprisingly different from those of *Neodryinus trinitatis* Richards, 1951, particularly in lacking the inner dorsal process from the paramere. Perkins (1906 : 484) has already noted that males of more than one species may happen to be bred from a single host species. Two cocoons associated with the type material are attached to the underside of a leaf and are more or less covered with white, waxy material, probably derived from the host. They are very flattened, closely adapted to the leaf-surface, oval, one (probably ♀) about 12 × 6 × 2 mm.; the other (not emerged) is somewhat smaller. The larval remains are not attached to the outside of the cocoon. The silk is white and, in the first one, moderately transparent. Through the irregular, 2 × 1 mm., emergence hole near one end it can be seen that there is an inner cocoon extending for most of the long axis but only 3 mm. wide.

It seems that there may be a group of species in the Malayan region closely resembling *N. lawanae*, or else that the species has already (though inadequately) been described several times.

1. *Neodryinus sumatranus* Enderlein, 1907 (Sumatra).

According to the description, this is very close to *N. lawanae*, but the vertex is said to be concave, and the mesoscutum and scutellum closely punctured rather than rugose.

2. *Phanerodryinus javanus* Roepke, 1916 (Java).

The description agrees very closely with *N. lawanae* but the enlarged claw is said to be simple. The proportions of the first five antennal segments are 35 : 17 : 93 : 56 : 55. In *N. lawanae* they are 35·5 : 16·1 : 93 : 58·2 : 42·1.

3. *Psilodryinus thoracicus* Fouts, 1922 (Palawan).

Apparently very close to *N. lawanae* but the femora and the anterior trochanters seem to be of a darker colour.

Neodryinus leptopus sp. n.

♀. Black; antennae brown, segments 1–2 whitish, 3–5 dark; mandibles (except ventral streak and tip), clypeus (except central black spot), malar space, large patch on gular region, fore coxa (except inner streak), fore trochanter (except dorsal streak), anterior streak on fore tibia, chela (except dorsal streak), four hind coxae (except dorsal spot), four hind trochanters, ventral streak on mid femur, dorsal spot on hind femur, tip of four hind tibiae, *whitish yellow*; mid and hind tarsi brown, last segment dark. Sides of pronotum posteriorly, tegula, tip of gaster, *testaceous*. Wings hyaline, fore wing with large basal band and inwardly sharply defined band across middle of pterostigma, reaching hind margin, *dark brown*. Veins dark, bases of long-veins and proximal half of pterostigma whitish. Length 5·5, length of fore wing 3·7 mm.

Body mainly shining, with inconspicuous pubescence, gaster smooth and shining; legs smooth and shining, only mid and hind femora inconspicuously punctured. Head with eyes in dorsal view rather more than twice as broad as long, posteriorly deeply emarginate, occiput little and obtusely produced behind the eyes. Clypeus roundly produced, not very transverse, ventral margin with strong excision. Malar space no longer than width of scape, without keel or furrow. Mandibles probably with four teeth, ventral one acute, more than twice as long as one next to it, mandible not swollen near its articulation. Frons and vertex smooth and shining towards side, disc finely shagreened, duller. Vertex deeply depressed between eyes which are very convex and strongly projecting, no occipital keel. Ocelli in a somewhat acute triangle (anterior angle 50° rather than 60°), POL : OOL = 1 : 5. Antennae extending back to about end of scutellum, a little thickened from end of segment 5, 1 distinctly curved, hardly twice as long as broad, 2 nearly cylindrical, more than half as long as 1, two and half times as long as broad, 3 one and a half times as long as distance between eyes at median ocellus, four times as long as 1, a little longer than 4 + 5, at least twelve times as long as broad, 4 eight times as long as broad, 4–9 becoming rather rapidly shorter, 9 about two and a half times as long as broad, hardly longer than 2, 10 as long as 7. Palpi not clearly visible. Pronotum pyriform, a little longer than broad in front, front with a fine margin, not lamellate, no emargination, back without margin, not lamellate, with shallow emargination, with a distinct though shallow impression just in front of it, a strong transverse impression at anterior quarter, only weakly humped behind this, part in front of impression smooth and shining, hump also shining but with regular longitudinal keels which cease before ventral margin, posterolateral corners rounded, not produced into lobes. Mesoscutum not quite twice as broad as long, moderately shining, with fine longitudinal rugae, especially behind, interstices somewhat shagreened, notaulices very feebly indicated. Scutellum flat, shining with reticulate rugae, separated from scutum by six well-defined pits. Postscutellum about one-third as long as scutellum with pits and striae. Propodeum shining, with coarse network of raised keels, all surfaces passing smoothly into one another, network coarser on sides and partly effaced posteriorly. Whole pleuron shining with a coarse reticulation of raised rugae. Fore coxa (fig. 11) very elongate, somewhat narrowed on distal half, six times as long as broad ; fore trochanter a little longer than coxa, almost as long as mid femur, distal third sharply clavate ; femur not much thickened, eight times as long as its greatest width, twice as wide as tibia which is three-quarters as long as tarsus ; tarsus with segment 1 cylindrical, as long as 4, apical bristles relatively short, five times as long as broad, 2 transverse with an anterior bristle bearing hook, 3 about twice as long as wide in ventral view, with proximal anterior hook, articulating part of 5 hardly quadrate ; chela extending back to end of segment 1, end not much hooked, with a row (possibly double) of long, rather dense white lamellae, distal group large and compact ; in one view chela much narrowed just before its end ; enlarged claw three-quarters as long as tarsus 5, nearly straight with distal sixth sharply incurved, inner surface feebly serrate with a row of twelve lamellae and a strong preapical tooth. Tibial spurs 1, 0, 2, longer one on tibia 3 about twice as long as width of tibia, shorter one about half as long. Hind femur strongly clavate, stalk forming distal half. Pterostigma very narrow, at least five times as long as broad, radial vein not angled and not emitting a coloured fold or vein. Gaster distinctly subpetiolate.

Type ♀, BORNEO : Kuching (*J. Hewitt*) (B.M.).

The species was given the above trivial name by P. Cameron but it seems that his description was never published. The specimen is a little mouldy and some of the sculpture is difficult to see.

The following key will separate the females of most of the species of *Neodryinus* Perk. Species known to me only from their descriptions are marked with an asterisk.

1. Tibial spurs 1, 0, 2. Enlarged claw with lamellae and a strong subapical tooth Subgenus **Leptodryinus** subg. n. (Type **Neodryinus** (**L.**) **leptopus** sp. n.)
 Pronotum with a weak transverse impression at anterior quarter, surface in front and below this smooth and shining. Eyes extremely prominent. Trochanter of fore leg four-fifths as long as mid femur. Antennal segment 3 longer than distance between eyes at median ocellus. Malaya . . . . **N. leptopus** sp. n.
–. Tibial spurs 1, 0, 1. Pronotal surface in front of impression never smooth and shining . . . . 2.
2. Enlarged claw with a row of distinct lamellae and a subapical tooth. Scutellum separated from the mesoscutum by a row of 5–6 large, well-defined pits . . . . Subg. **Neodryinus** Perkins 3.
–. Enlarged claw with at most some very minute bristles Subg. **Prodryinus** Kieffer 8.
3. Gaster microscopically sculptured, not shining. Wings with three dark bands. Dorsum of head reddish-brown with a black central area. Antennae yellow. New South Wales . . . **N. trilineatus** Dodd, 1914*

–. Gaster shining. Wings with two dark bands. Dorsum of head black . . . 4.

4. Pronotum with no transverse impression. Segment 1 of fore tarsus longer than 4. Antennae reddish. Brazil . . . **N. affinis** (Arlé, 1935)*

–. Pronotum with a distinct transverse impression . . . . 5.

5. Larger species, length 8.0 mm. Fore tarsus with enlarged claw with a very large subapical tooth, segment 1 longer than 4. Madagascar **N. gigas** Ceballos, 1936*

–. Smaller species, length not much more than 5·0 mm. Enlarged claw of fore tarsus with a small subapical tooth. Queensland . . . . 6.

6. Head above more or less shining, finely striate. Segment 1 of fore tarsus shorter than 4. Antennae pale, segment 3 longer than distance between eyes at median ocellus . . . . **N. koebelei** Perkins

–. Head above dull. Antennal segment 3 hardly longer than distance between eyes at median ocellus . . . . 7.

7. Antennae black, except scape beneath and segments 7–10. Segment 1 of fore tarsus as long as 4. Mesoscutum more coarsely rugose **N. nelsoni** Perkins

–. Antennae pale brown, segment 6 often darker. Segment 1 of fore tarsus a little shorter than 4. Mesoscutum granulate . . **N. raptor** Perkins

8. Pronotum without a transverse impression, surface, including sides below posteriorly, finely granulate. Fore tarsus (fig. 10) with the enlarged claw with a small subapical tooth, three-quarters as long as tarsal segment 5; segment 1 as long as segments 2 + 3 + 4. Trinidad . . . . **N. trinitatis** Richards

–. Pronotum with a distinct transverse impression . . . . 9.

9. Enlarged claw only half as long as tarsal segment 5, strongly curved without bristles or subapical tooth. Pronotum finely striate, a little shining in front. Scutellum separated from the feebly striate mesoscutum by a wide, shallow, crenate furrow. Antennae and sides of pronotum pale brown . . . . **N. acuticollis** (Kieffer)

–. Enlarged claw at least two-thirds as long as tarsal segment 5 . . . 10.

10. Pronotum in front of transverse impression shining and quite coarsely striate, its sides widely yellow. Scutellum and mesoscutum separated by a wide, crenate furrow. Head not depressed between the eyes . 11.

–. Pronotum dull and granulate, at most very finely striate at sides anteriorly . . . . 14.

11. Antennae black with at least segments 4 and 5 clear testaceous. Mesoscutum longitudinally rugose. Enlarged claw with a few bristles and a small subapical tooth. Arizona . . . . 12.

–. At most one central antennal segment paler than those on each side of it. Mesoscutum not distinctly longitudinally rugose . . . . . . 13.

12. Antennae black, segments 4–5, part of 3, and 1 beneath, testaceous **N. arizonicus** Perkins*

–. Antennae black, segments 1, 3–5, and part of 6 ferruginous **N. dubiosus** Perkins*

13. Mesoscutum dull and rather finely rugose. Clypeus black, except for a small patch on each side. Antennae dark, scape beneath and segment 5 pale, segment 4 shorter than 1. Enlarged claw quite simple, chela distinctly hooked at its end. Panama . . . **N. alticola** (Cameron)

–. Mesoscutum somewhat shining, with a smooth patch on each side posteriorly. Clypeus yellow. Antennae with segments 1–4 yellow, 5–10 darker, segment 4 longer than 1. Enlarged claw with a few bristles and a strong subapical tooth. U.S.A. . . . . **N. ormenidis** (Ashmead)

14. Mesoscutum and scutellum with strong, longitudinal rugosities, and separated by 5–6 ill-defined pits. Antennae, clypeus, legs and gaster red-brown. Sides of pronotum yellow. Head distinctly depressed between the eyes. Antennal segment 4 about as long as 1. Enlarged claw with no bristles but with a minute subapical tooth. S. Africa **N. rugidorsalis** (Turner, 1928)

–. Mesoscutum and scutellum granulate or if (*N. brachycerus*) with fine rugae, then scutum and scutellum separated by a narrow, shallow furrow and the gaster black . . . . 15.

15. Abdomen red-brown. Mesoscutum and scutellum separated by one large pit on each side and 3–4 small ones in between them. Scutum and scutellum granulate, sides of pronotum black. Head somewhat depressed between the eyes, distinctly striate. Antennae black, segment 1 white beneath, articulations of 2 and 3, and whole of 8–10, brownish; segment 3 as long as 4 + 5. Enlarged claw with an acute subapical tooth and some fine hairs. Malaya . **N. lawanae** sp. n.

–. Gaster black, at least above. Head almost flat between the eyes, not striate . . . . 16.

16. Sides of pronotum yellow, gaster dark reddish at sides. Mesoscutum granulate, with appressed silvery pubescence. Clypeus yellow. Antennae with segments 1–4 pale yellow, 5–7 black, 8–10 brown, 3 as long as 4 + 5. Enlarged claw with a subapical tooth beyond which is a minute leaf-shaped bristle. Panama . **N. maculicornis** (Cameron)

–. Pronotum and gaster black. Mesoscutum and scutellum with fine rugae, pubescence inconspicuous. Clypeus dark. Antennae brown, with segment 1 white, 2–3 paler than 4–10, 3 one and a half times as long as 4 + 5. Enlarged claw strongly curved, simple. Argentina **N. brachycerus** (Kieffer)

Doubtful species of *Neodryinus* Perk., including species which have been referred to *Prodryinus* Kieff. and *Psilodryinus* Kieff.:

1. *Neodryinus sumatranus* Enderlein, 1907. (See p. 66.)
2. *Phanerodryinus javanus* Roepke, 1916. (See p. 66.)
3. *Psilodryinus thoracicus* Fouts, 1922. (See p. 66.)
4. *Neodryinus japonicus* Uchida, 1927. Japan. This may perhaps be correctly placed, though the description is inconclusive. If it is, it probably belongs to *Neodryinus s.s.*, since the enlarged claw bears spine-like lamellae.
5. *Psilodryinus carinatus* Fouts, 1924. Pennsylvania. Clearly belongs to the subgenus *Prodryinus*. The enlarged claw is long with a minute subapical tooth.
6. *Dryinus nigrellus* Brues, 1904. New York. This species possibly belongs to *Neodryinus* Perk.
7. *Psilodryinus reticulatus* Fouts, 1922. Luzon. I cannot place this species with certainty, but the three raised lines on the mesoscutum would make it very different from any other species of *Neodryinus* Perk.
8. *Neodryinus somniatus* Brues, 1933. Baltic Amber. This must belong to some other genus since the hind angles of the pronotum are strongly produced backwards and the postscutellum (= metanotum) is not very short.
9. *Neodryinus erraticus* Turner, 1928. S. Africa. According to the type in the collection of the British Museum, this species belongs to the Dryininae.

10. *Dryinus ruficeps* Cameron, 1888. Panama. This belongs to the Dryininae, and is peculiar in that the median ocellus is enlarged and very far in front of the other two, making the ocellar triangle acutely isosceles.
11 and 12. *Dryinus draco* Marshall, 1905, and *D. dracunculus* Marshall, 1905. Spain. These two species probably do not belong to *Neodryinus* Perk.
13. *Mystrophorus americanus* Ashmead, 1887. Florida. Genus doubtful.
14. *Dyrinus bifasciatus* Say, 1828. Indiana. Genus doubtful.
15. *Prodryinus striaticeps* Kieffer, 1909. Brazil. This was later made the type species of *Tridryinus* Kieffer, 1913. Probably really belongs to the Dryininae, since the pronotum appears to have posterior lobes and mesoscutum complete notaulices.
16. *Dryinus stantoni* Ashmead, 1904. Manila. According to Fouts (1922: 629) this is a *Dryinus* Latr. (= *Lestodryinus* Kieffer).

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THE ECOLOGY OF *GLOSSINA PALPALIS* IN NORTHERN NIGERIA.

By T. A. M. NASH, O.B.E., D.Sc.(Lond.)
(*Chief Entomologist, West African Institute for Trypanosomiasis Research*)

and

W. A. PAGE, B.Sc., A.R.C.S.
(*Research Entomologist, W.A.I.T.R.*).

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PART I—INTRODUCTION.

1. HISTORY OF INVESTIGATION.

TOWARDS the end of 1944 the senior author, who was then Medical Entomologist to the Nigerian Sleeping Sickness Service, established a small field station at Katabu and started a long term investigation into the ecology of *G. palpalis*.

In April, 1947, Mr. N. F. Bowers, Development Officer, was posted to Katabu, where he rendered valuable assistance.

In April, 1948, when the plan to establish the West African Institute for Trypanosomiasis Research had advanced sufficiently, the senior author was appointed Chief Entomologist and the work at Katabu was taken over by the new research organisation. In October, 1949, the junior author took over immediate charge of the field station, and, assisted by Mrs. M. Page, B.Sc., remained in charge until the investigation was closed in March, 1951.

2. SITUATION AND DESCRIPTION OF THE KATABU AREA.

Katabu (10°42′ N., 7°31′ E.) is situated 14 miles N.N.E. of Kaduna, which is the capital of Northern Nigeria ; the altitude is about 2000 ft. above sea level. The country is gently undulating ; the soil is lateritic.

Katabu lies in the centre of Keay's Northern Guinea vegetation zone (Keay, 1949), which he describes as " a western extension of the great ' Miombo ' woodlands (*Isoberlinia-Brachystegia*) of East, Central and South Tropical Africa." It is continuous with similar woodland in the Anglo-Egyptian Sudan. Around Katabu, *Isoberlinia doka*, *I. tomentosa*, *Monotes kerstingii*, *Daniellia oliveri* and *Uapaca somon* are characteristic species of the savannah. Grass growth normally attains a height of about 4–5 ft. in October, but in the valley bottoms it may be up to 8 ft. ; most of the grass is burnt in December.

The country is intersected by streams which are fringed with the usual distinctive forest, characterised by an evergreen understorey of forest shrubs and climbers, above which stand widely spaced emergent trees of savannah affinity, e.g., *Vitex doniana* and *Khaya senegalensis*. This fringing forest, which forms the habitat for *G. palpalis* and *G. tachinoides*, may be only a few yards in width ; nevertheless, it stands out darkly and strikingly, in contrast with the adjacent woodland savannah. This paper describes the results of a study of the specialised climate and vegetation of one of these linear habitats of *G. palpalis*—habitats which enable this humidity-loving tsetse to exist within, and hence to traverse, the arid woodland savannah belt.

In the longitude of Katabu the northern limit of *G. palpalis* is only 10 miles further north than the stream where these studies were made ; hence we were observing conditions at the extreme hot, dry end of the range of this species.

The bulk of Nigeria's human trypanosomiasis, and much cattle trypanosomiasis, is transmitted by the riverine species of tsetse living under conditions such as those described above. Contact is made when man and his animals water at the streams ; both man, his animals and the tsetse are all equally dependent on the stream, especially in the late dry season. A common feature of this association is the low density of tsetse flies (Nash, 1944); hence in selecting a stream for this research, it would have been atypical had a stream been chosen with a very high fly density. It seemed to be more important to select a typical stream with medium low fly density than an exceptional stream with a swarming fly population; but the natural result of this decision was to make research work extremely difficult owing to the low fly numbers, an obstacle that was surmounted by extending the investigation over six years and sometimes grouping the data.

The chief reason for selecting Katabu was the presence of a typical stream within an *uninhabited* forest reserve. Here the flies were unlikely to be infected with trypanosomes pathogenic to man, thus obviating the risk of the fly boys becoming demoralised by the occurrence of cases of sleeping sickness; further, in a reserve there was no risk of encroachment on the riverine vegetation by farmers and wood cutters.

Although *G. tachinoides* also occurred in this stream, the numbers were very small; it was pre-eminently a habitat of *G. palpalis*.

3. THE SEASONS.

There is one dry and one wet season. The meteorological data given in this section refer to readings at 4 ft. above ground-level, taken in our open woodland station.

The Dry Season (November to March).

The dry season may be considered to last for 5 months. During six years of observations the four months from November to February inclusive were virtually rainless, and the average for March was only half an inch (see Table I).

Table I.—*Average monthly rainfall over 6 years at Katabu*, 1945–'50.

Months.	XI.	XII.	I.	II.	III.	IV.	V.	VI.	VII.	VIII.	IX.	X.	Annual average.
Average rainfall (inches)	0·0	0·0	0·0	·1	·5	2·5	5·0	7·1	7·5	11·7	9·3	2·9	46·6

1. The early dry season or cold season (November–January): In November the country rapidly dries up when the south-west monsoon gives place to the desiccating Harmattan wind; the nights become cold, but the days remain hot.

Normally the maximum temperature remains high, averaging about 90° F. (32·2° C.), but in exceptional years the Harmattan haze may be so heavy that the maximum temperatures are reduced. Very low minimum temperatures occur near dawn averaging 53–56° F. (11·7–13·3° C.), but sometimes falling as low as 42·5° F. (5·8° C.). Owing to these low night temperatures the *mean* temperature is abnormally low, ranging between 71° and 72° F. (22° C.) in December and January. The normal combination for this season of high day temperatures and low night temperatures produces an enormous temperature range; in December a range of 50·5° F. (28° C.), from 42·5° to 93° F., has been recorded between 6 a.m. and 3 p.m. of the same day.

Whilst the mean temperature remains fairly constant throughout this season, the evaporation rate soars progressively upwards. The grass is burnt during December and January.

2. The late dry season (February and March): The temperature starts to rise in February. In March the highest maxima occur, temperatures up to 103° F. (39·4° C.) having been recorded with a mean monthly maximum reaching 96·4° F. (35·8° C.). March is also the month with the most extreme degree of atmospheric dryness. The mean daily evaporation rate for this month, using a Livingstone white atmometer sphere, may reach 98 c.c. With afternoon temperatures ranging from 92–102° F., it is not unusual to get relative humidities as low as 10–15 per cent. This combination of high temperature and very low humidity makes the late dry season one of stress for the tsetse population.

The Wet Season (*April to October*).

Over 6 years the annual rainfall ranged from 41·2 to 50·6 in., and averaged 46·6 in. (1184 mm.), of which 21 in. fell in August and September (Table I); the average number of wet days was 80.

1. The early rains (April and May): At this season the days remain very hot, and the nights become much warmer, resulting in the year's highest mean monthly temperatures of about 81–82° F. (27·5° C.). The prevailing wind, which has veered round to the south-west, is laden with moisture and the first tornadoes occur, resulting in a great drop in the evaporation rate and rise in the humidity. The weather is no longer hot and dry, but hot and humid. As the storms become more frequent the maximum temperature falls and the humidity rises.

2. The heavy rains (June–September): The rainfall increases gradually until a peak is reached in August, or sometimes in September; the heaviest rain occurs in these two months, when the mean monthly temperature is relatively low at about 76° F. (24·4° C.) with a relative humidity of about 90 per cent.

3. The end of the rains (October): The rains end abruptly during this month, which suddenly becomes very hot and remains unpleasantly humid; on some days the temperature may reach 95° F.

4. DESCRIPTION OF THE INVESTIGATION.

(a) The Main Katabu Fly-round.

A native trade route traverses the Anara Forest Reserve and crosses the Bahago stream 1½ miles from its source. In October, 1944, the main fly-round was marked out along the stream bank on either side of this ford; it tapped 1800 yards of fringing forest. This distance was divided into three sections, named the Red, White and Blue Sections because it was intended to mark the flies caught in each section with these colours. The limits of the sections were determined by changes in the character of the fringing forest.

Each section was subdivided into 100-yard-long " sub-sections," in order to ascertain any localised fly preferences, and to facilitate an analysis of the vegetation and other factors that might account for such preferences.

Meteorological instrument stations were set up in the Red and White Sections, and a third station in the adjacent woodland savannah (see fig. 1).

(b) The Subsidiary Katabu Fly-rounds.

It was decided to augment the main fly-round with an up-stream and a down-stream observation post, so that any movements of marked flies from the main round could be recorded. Catches in the down-stream or Yellow Section were started in November, 1944, at a point 1467 yards below the Blue Section, and in the up-stream or Green Section in July, 1945, at a point 1350 yards above the Red Section. Each of these subsidiary sections was 300 yards in length.

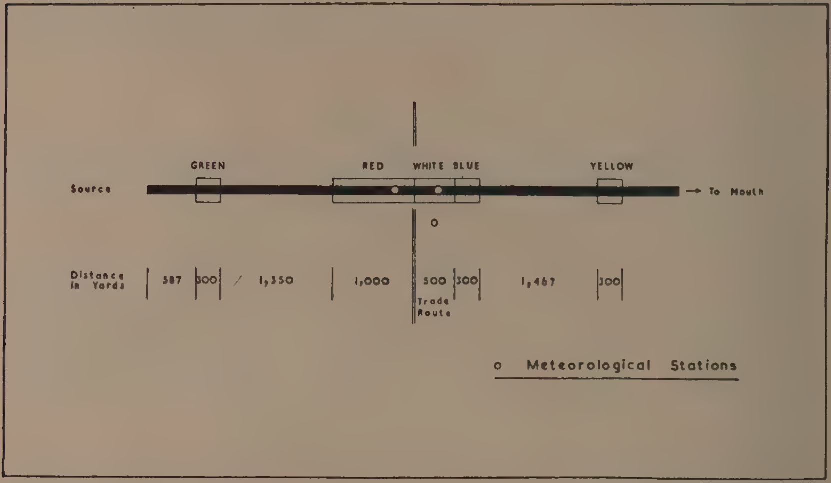

Fig. 1.—Scale diagram of fly-round lay-out on Bahago stream.

Hence moving down-stream the order of the sections was as follows :

Green—Subsidiary
Red
White } Main Fly-Round
Blue
Yellow—Subsidiary

(c) Summarised Characteristics of each Katabu Section.

The main characteristics of each section upon which their delimitation was based are noted below. The width of the fringing forest is measured from the junction of forest and savannah on one bank, across the stream-bed, to the reappearance of the savannah on the opposite bank. The presence of the palm *Raphia sudanica* is considered to be an excellent indicator of the damper type of forest.

The Green Section.

Length.—300 yards.
Width of fringing forest.—Average = 97 yds. Max. = 150 yds.
Stream.—No permanent pools. Banks ill-defined, 3–4 ft. deep. Localised creeper tunnel.
Raphia.—Dominant.
Characteristics.—Extensive, evergreen fringing forest sharply demarcated from savannah by wall of insulating vegetation. Below isolated emergents, 60 to 70 ft. high, there is a canopy at 40 to 45 ft.; beneath this is an understorey which ranges from clumps of impenetrable evergreen thicket to low umbrella-like creeper tangles, to open glades under high shade. *An ideal, major permanent habitat of* G. palpalis, *typical of the damper, evergreen type of extensive fringing forest.*

The Red Section.

Length.—1000 yds.
Width of fringing forest.—Average = 10 yards. Min. = 5 yds.
Stream.—Some permanent pools. Banks well defined, 5½–9 ft. deep. Creeper-tunnel usually present.
Raphia.—Fairly common.
Characteristics.—Very narrow fringing forest, generally demarcated from savannah by wall of insulating vegetation. Below emergents, 35–40 ft. high, which sometimes form a canopy, is the tangle which roofs over the stream. *Typical of the restricted minor permanent habitats as found at village water holes.*

The White Section.

Length.—500 yds.
Width of fringing forest.—Average = 47 yds. Max. = 55 yds.
Stream.—No permanent pools. Banks ill-defined and shallow; sometimes several channels. Creeper-tunnel rare.
Raphia.—Absent.
Characteristics.—In main, a belt of mixed-deciduous forest merging into the savannah, with *no* wall of insulating vegetation. Below a canopy 50 to 80 ft. high is a light understorey of shrubs. (*N.B.*—At the far end there is no canopy, but mixed-deciduous thicket.) *Typical of favourable temporary habitats which enable the fly population to recover from the adverse effects of the dry season.*

The Blue Section.

Length.—300 yds.

Width of fringing forest.—Average = 34 yds., but never more than 6 yds. on the north bank which faces the desiccating Harmattan wind.

Stream.—No permanent pools. Banks well defined, but one high and the other low. Localised, deciduous creeper-tunnel, but sometimes completely shadeless.

Raphia.—Absent.

Characteristics.—A belt of deciduous secondary thicket frequently interrupted by the incursion of grass; an occasional giant emergent. *Typical of very unfavourable temporary habitats, associated with old farmland or neglected clearings.*

The Yellow Section.

Length.—300 yds.

Width of fringing forest.—Average = 65 yds. Max. = 80 yds.

Stream.—No permanent pools. Banks well defined, 5–8 ft. deep. No creeper-tunnel.

Raphia.—Rare.

Characteristics.—Extensive mixed-deciduous forest merging into the woodland, with *no* wall of insulating vegetation. Emergents up to 70 ft. tower above a well-developed understorey of trees, 15–25 ft. high, with crowns interwoven with climbers to form an excellent canopy; beneath this the ground is fairly open and covered with herbs, but there are occasional thickets and patches of shrubbery. *Typical of very favourable temporary habitats.*

(d) The Fly-round Technique Employed.

The fly-rounds were carried out as follows:

Green Section:	14th day of each month	1st period.
	15th ,, ,, ,,	
	29th ,, ,, ,,	2nd period.
	30th ,, ,, ,,	
Main Round:	12th ,, ,, ,,	1st period.
	13th ,, ,, ,,	
	27th ,, ,, ,,	2nd period.
	28th ,, ,, ,,	
Yellow Section:	As for Green Section.	

On the first day of a period the catching would start at the beginning of a section, but on the second day it would start at the end and work backwards, thus preventing the first subsection from always being visited early in the morning. Each section was visited 4 times per month, with a fortnight's interval between the two periods.

All tsetse caught were marked with artist's oil paints and liberated. The metathorax was reserved for the locality, i.e., for the colour of the section in which the fly was found; the mesothorax was left blank and the prothorax was reserved for the date. The date was indicated by one mark on the left side of the prothorax showing the month's colour, and by either a red or a white mark on the right side of the prothorax, according as to whether it was the first or second period of the month. This very simple system made errors virtually impossible.

The catching team consisted of five men, viz.,

2 catchers, who kept well in front;
1 caller, who acted as an intermediary;
1 marker and 1 recorder who kept out of sight in the background.

The caller would take the fly back from the catchers to the marker and recorder, and would call out sex, state of nutrition, and colours if previously marked; the recorder, who entered the data, would check the marks before the fly was released.

(e) The Jaji Control Fly-Round

This control round was set up on a stream 10 miles further north—the most northerly *palpalis* habitat in the Katabu longitude. It is a typical northern Nigerian stream, all of which dries up excepting for 600 yds. of permanent pools, upon which both the town of Jaji and the tsetse are dependent in the late dry season. The round was 1,400 yds. long and subdivided into three sections. The same technique was used as that already described; the Jaji round was carried out on the 7th and 8th, and 21st and 22nd of each month.

The sole reason for this round was to check that seasonal fluctuations in fly density, etc., as recorded at Katabu were not atypical; this was deemed necessary because at Katabu the stream flows through uninhabited forest reserve so that the flies are dependent mainly on game, and not on man as at Jaji. Since little mention of the Jaji round will be made in this paper, no vegetational details will be given.

PART II—THE SEASONAL FACTOR.

1. INTRODUCTION.

In the past there have been instances where, owing to the lack of field studies on the climate of the tsetse's environment, painstaking laboratory experiments have been carried out under conditions of temperature and humidity which would rarely be encountered in the field.

The subject of the tsetse's climatic environment, both pupal and adult, has developed a special significance since Burtt (1946*a*) showed that *G. morsitans* adults, bred from pupae incubated at a high temperature, are more readily infected with *T. rhodesiense* and also transmit more readily than flies bred from pupae kept at a lower temperature. Subsequently, Fairbairn and Culwick

(1950) confirmed and amplified Burtt's work on the pupal temperature, and also showed that the temperature of fly maintenance was important in the case of the *female* of *G. morsitans*. Earlier workers had noted that the percentage of wild *G. morsitans* infected with trypanosomes rose in the hot weather (Kinghorne *et al.*, 1913 ; Chorley, 1929) ; further, Taylor (1932) found that by incubating adult *G. tachinoides* during the period when they were being fed on *T. gambiense*-infected hosts he could raise the infection rate considerably.

If the laboratory worker is to make deductions applicable to the field, he must know the climatic conditions experienced by the tsetse and its pupa. This is one of the reasons why we have striven to accumulate extensive data on the ecoclimate of *G. palpalis*, as it is to be hoped that laboratory workers will repeat the experiments of Burtt, Fairbairn and Culwick on this species of tsetse.

* * * *

As already mentioned, three meteorological stations were set up near the centre of the main fly-round, as under:

The Open Woodland Station.—This permanent station was sited about 100 yds. outside the fringing forest in the open woodland which slopes up from the stream. It was intended to give standard readings for comparison with other parts of Nigeria, to give readings for comparison with the ecoclimate within the adjacent stream, and incidentally to provide data upon the climate enjoyed by *G. morsitans* in this part of Nigeria. (*N.B.*—A few *G. morsitans* infiltrated into this area every wet season from adjacent fly belts of similar woodland.)

The White Section Station.—This permanent station was sited in the stream-bed about 100 yds. east of the ford ; but in the wet season the instruments had to be moved on to an adjacent mound, still within the fringing forest, to prevent their destruction by occasional spates of flood water. This station illustrated the climate in a section of the stream which, on drying up, was evacuated by *G. palpalis* in favour of the Red Section.

The Red Section Station.—Occasional spates made it too dangerous to keep instruments anywhere within the narrow fringing forest of this section during the heavy rains. Hence it had to be a temporary station set up in November, at the beginning of the dry season, and closed before the heavy rains in June. The initial site was at a point about 100 yds. west of the ford, but as the season advanced and the water dried up the instruments always had to be moved up-stream *so that they could be kept in the vicinity of water.* A movable meteorological station may sound a novel idea, but the main purpose of this investigation was to study the climate in which *G. palpalis* lived, and since, as will be shown later, this tsetse is forced to keep near water in the late dry season, unless the vegetational insulation is adequate, it was essential to record the climate in which the fly survived the dry season.

Since climatic data for White Section would be irrelevant at those seasons when it had been evacuated by tsetse, it became necessary to build up a "composite climate"—a climate composed of White Station data from June to November inclusive, and of Red Station data from December to May. By subdividing the year at these times the transfer occurs at seasons when readings from the two stations are very similar.

Temperature and saturation deficit readings were taken from recording thermohygrographs kept in Stevenson screens. The mean temperatures were obtained from maximum plus minimum readings divided by two; it was found that under local conditions these results were almost identical with those got by the laborious planimeter method. The evaporation rate was measured with Livingston white atmometer spheres.

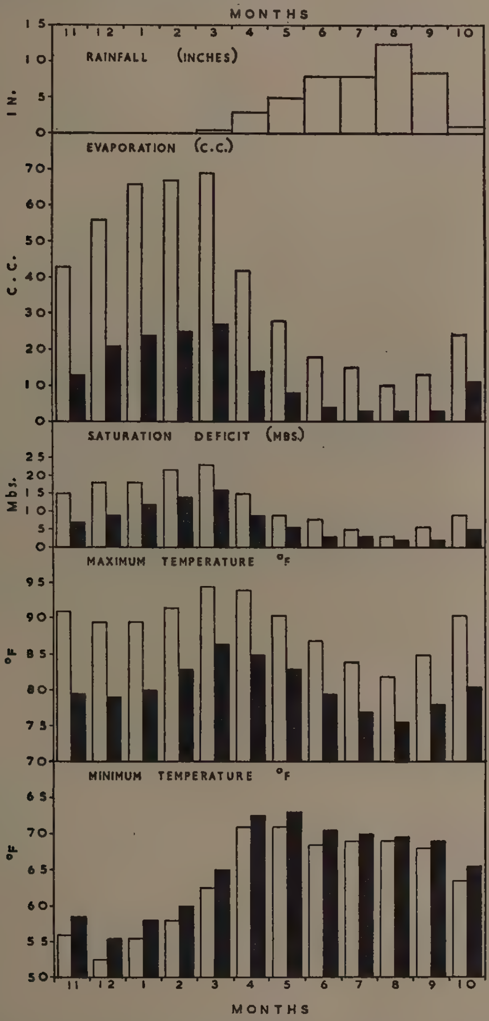

FIG. 2.—The climate of the open woodland (white), compared with the composite stream-bed climate in which *G. palpalis* lives (black).

(From mean monthly climatic data collected over 3 years, 1947–1949, at 4 ft. above ground-level.)

2. A COMPARISON OF THE CLIMATE IN THE WOODLAND, AND IN THE STREAM-BED WITHIN FRINGING FOREST.

The average monthly figures over three years for the various climatic factors measured at four feet above ground-level are shown in fig. 2, where the open woodland and composite stream-bed climates can be compared. The late dry seasons of these three years were the mildest recorded in the six years of observations. The graphs start in November—the first month of the dry season.

The evaporation rate.—There is an enormous disparity between the evaporation rates of the two environments, but in the open woodland the atmometer bulb is exposed to full sun-light, whereas within the fringing forest there is only dappled sun-light.

The evaporation rate is much lower in the stream-bed. At the start of the dry season it is 30 c.c. less (43 : 13), at the end of this season it is 42 c.c. less (69 : 27); at the beginning of the rains it is 28 c.c. less (42 : 14) and in the height of the rains 7 c.c. less (10 : 3).

The saturation deficit.—These data are obtained from two thermohygrographs *similarly* housed in Stevenson screens; even so there is a very considerable difference between the two environments. The saturation deficit is lower in the stream-bed. Throughout the dry season it is 6 to 9 mb. less (18·4 : 12·2 and 18·0 : 9·3), but by the height of the rains the difference is only 1·5 mb. (3·2 : 1·7).

Temperature.—The maximum temperature is considerably higher in the open woodland. At the beginning of the early dry season the stream-bed is 12° F. (6·7° C.) cooler, in the late dry season 8° F. cooler, and in the heavy rains 7° F. cooler.

There is very little difference between the minimum temperatures in the two environments; the stream-bed is some 2–3° F. *warmer*. This should be remembered because it signifies that the lower *mean* temperature of the stream-bed is solely due to the lower maximum temperature.

Conclusions.

1. There is a definite ecoclimate within the fringing forest which is much less severe than the general climate of the adjacent woodland.

2. Readings at 4 ft. above ground-level show that the temperature in the stream-bed does not rise nearly as high in the day time or fall quite so low at night; hence the temperature range is much less than in the woodland—the average range over a month may be 14° F. (7·8° C.) less in the stream-bed.

3. Both the evaporation rate and saturation deficit are considerably less in the stream-bed, the difference being considerably greater in the dry season.

3. THE COMPOSITE CLIMATE WITHIN THE STREAM-BED AT FOUR FEET AND FOUR INCHES ABOVE GROUND-LEVEL.

In an endeavour to show whether the environment of *G. palpalis* was covered by the two heights—4 ft. and 4 in.—at which meteorological records had been collected, a small investigation was recently made into the resting heights of this tsetse. In April, 1951, when the temperature was still high but the humidity had started to rise because the first rain had fallen, the mean resting height of the 20 flies found was 2·9 ft.; but out of 71 flies found at rest during the ensuing wet season the mean monthly resting height had risen, ranging between 3·7 and 3·9 ft. Since *G. palpalis* probably rests at still lower heights in the very dry, hot weather, it is believed that the data collected at 4 ft. and 4 in. *does* cover the range of climate in which the fly lives. Admittedy there are brief interludes when the fly may enter the adjacent woodland in search of food, or may sun itself on the edge of the fringing forest especially in the height of the rains.

Table II.—*The range of climate available to* G. palpalis *throughout the year in its natural habitat.*

Average mean monthly data during 2 years for the composite stream-bed climate at 4 ft. and 4 in. above ground-level.

Month.	Maximum temperature (° F.).	Minimum temperature (° F.).	Temperature range (° F.).	Mean temperature (° F.).	Relative humidity % at mean (temp.)	Evaporation (c.c.).	Saturation deficit (mb.).	Season.
Nov. .	79·5–74·5	58·0–59·0	21·5–15·5	69·0–66·0	69–73	13·0– 7·5	7·4– 5·9	Early dry
Dec. .	79·5–75·0	55·5–56·5	24·0–19·5	67·5–65·0	54–60	24·0–18·0	10·4– 8·3	
Jan. .	80·5–77·0	57·5–58·0	23·0–19·0	69·0–67·5	49–54	25·0–18·5	12·3–10·3	
Feb. .	82·5–77·5	59·5–60·5	23·0–17·0	71·0–69·0	43–52	28·0–23·0	14·5–11·5	Late dry
March .	86·0–81·5	66·5–66·5	19·5–15·5	76·0–74·0	50–57	27·0–21·0	15·3–12·0	
April .	84·5–82·0	72·5–70·5	12·0–11·5	78·5–76·5	74–79	13·0– 7·0	8·5– 6·5	Early rains
May .	81·5–79·5	72·5–72·5	9·0– 7·0	77·0–76·0	85–86	7·0– 4·5	4·8– 4·3	
June .	79·5–78·0	69·5–69·5	10·0– 8·5	74·5–73·5	89–94	5·0– 2·5	3·1– 2·5	Heavy rains
July .	77·0–77·0	69·5–69·0	7·5– 8·0	73·5–73·0	89–94	5·0– 1·5	3·0– 1·7	
Aug. .	76·0–75·5	69·0–68·5	7·0– 7·0	72·5–72·0	94–94	4·0– 1·0	1·7– 1·7	
Sept. .	78·0–77·5	68·5–69·0	9·5– 8·5	73·5–73·0	91–91	4·0– 1·5	2·6– 2·6	
Oct. .	80·0–78·5	65·0–65·5	15·0–13·0	72·5–72·0	82–86	11·0– 6·0	4·9– 3·8	End of rains

(*N.B.*—In every case the first column refers to 4 ft. and the second to 4 in.)

Under each climatic factor recorded in Table II the figures in the first column were collected at 4 ft. above water and those in the second column at 4 in.; within these limits the fly can select what climate it prefers.

The two years upon which these data were based were the two mildest years of the investigation. This selection was not deliberate but enforced, because only for these two years were all our monthly records complete for all the factors shown. In other years, owing to the breakdown of thermohygrographs necessitating their replacement by maximum and minimum thermometers, there were short gaps in our humidity and saturation deficit readings. But since we were working at the extreme hot, dry end of the range of the species, the data from mild years will be of wider application. As will be shown on p. 87, even in the most severe dry seasons there is little deviation from the figures shown in Table II for 4 in.; but at 4 ft. the difference may be considerable, as will be shown later in Table III.

An inspection of Table II will show that in such mild years the range of climate available to *G. palpalis* at the two heights is not very great.

Temperature.—By settling at the lower height in the dry season, the fly can obtain a relief of up to 5° F. (2·8° C.) in the mean maximum temperature, of up to 3° F. in the mean temperature, and a temperature range that is 4° to 6° F. less. In the rains the difference between the two heights becomes negligible.

Reference to Table II will show that the minimum temperatures are almost identical at the two heights ; hence differences in the mean temperature must be mere reflections of the differences in the maximum temperature.

Saturation deficit, relative humidity and evaporation.—By settling at the lower height the fly can obtain a relief of up to 3·3 mb. (2·5 mm.) of saturation deficit or 6·5 c.c. in the evaporation rate. In the heavy rains the difference becomes less.

Even though the dry season data are for the two mildest years and even though the Stevenson screens were either 4 ft. above water or 4 in. above wet sand, it will be noted that in February *G. palpalis* would have been unable to find a mean relative humidity higher than 52 per cent. at 69° F.

Mellanby (1936) undertook a series of experiments on *G. palpalis* with relative humidities of 88, 65, 44 and 19 per cent., with the temperature constant at 75° F. He showed that at 65 per cent. R.H. the flies are in no danger of desiccation, and that the percentage survival of flies over 30 days was almost identical at both 88 and 65 per cent. R.H. However, at the lower humidities of 44 and 19 per cent. the flies do suffer from desiccation and the number of flies surviving 30 days is very small ; but, in a second experiment at 44 per cent. R.H. he found that by the special coaxing of the very thin flies to make them feed he could raise the survival rate for 30 days from 3 per cent. to 80 per cent. These results suggest that at 75° F. a relative humidity of 44 per cent., or lower, is unfavourable to longevity unless game is extremely abundant.

At Katabu game is scarce, so that in January, February and March when even in mild years the *mean* relative humidity of the stream-bed ranges between 43 and 57 per cent., it is reasonable to suppose that flies may be suffering from desiccation and that longevity is likely to be reduced ; this is especially likely when one remembers that for many hours of the day the humidity must be far lower than the mean figures quoted. For example, in severe years it has been found that in the afternoons the relative humidity may be as low as 19 per cent. at 4 ft. and 23 per cent. at 4 in., with temperatures of 92° and 89° F. respectively. (The small difference between the *absolute* humidities at the two heights will be explained on p. 86.) Later it will be shown that longevity is indeed reduced in these months.

Returning to Table II, it should be noted that in the rains the atmosphere is nearly saturated, even at some distance above ground-level.

* * * *

Geigy (1948) found that the optimum condition for breeding and maintaining a colony of tsetse in his laboratory in Switzerland was to keep the temperature constant at 79° F. (26° C.) and the relative humidity at 85 per cent., a combination which gives a saturation deficit of 5 millibars. It will be noted that his constant temperature of 79° F. is higher than any mean monthly temperature shown in our Table II. This is not so curious as it may appear, because, as will be shown later, p. 138, the climatic conditions around the month of May are the most favourable of the whole year, both for a high reproduction rate and for a maximum expectation of adult life. If we take an average of the mean monthly readings shown in Table II for April, May and June at 4 ft.—the most appropriate height for this season—we find that the most favourable conditions in the field are represented by a mean temperature of

77° F. (25° C.) with a relative humidity of 83 per cent., cf. Geigy's 79° F. and 85 per cent.

Although irrelevant to the theme of this paper, we have in Appendix I reproduced a table which incorporates some of the Katabu climatic data for *G. palpalis* used in Table II, together with similar data for *G. tachinoides* obtained between 1934 and 1936 at Gadau—which is in north-eastern Nigeria. In both cases the data were collected at the hot-dry end of the respective ranges of the two species. It will be seen that *G. tachinoides* can withstand a much more severe climate than *G. palpalis.*

Conclusions.

1. In years with mild dry seasons the climate at the pools is a little less severe at 4 in. than it is at 4 ft.

2. Even in such mild years and by the pools, during the latter part of the dry season the *mean* relative humidity ranged between 43 and 57 per cent., with mean temperatures between 67·5° and 76° F.; for many hours of the day the relative humidity must have been much lower. In view of the work of Mellanby (1936) and the scarcity of game at Katabu, the flies should have been suffering from desiccation and reduced longevity.

3. Our field results suggest that the optimum conditions for rapid breeding and long adult life are represented by a mean temperature of 77° F. (25° C.) with a relative humidity of 83 per cent., cf. 79° F. and 85 per cent., as found by Geigy (1948) in the laboratory.

4. THE MOST EXTREME METEOROLOGICAL READINGS RECORDED DURING SIX YEARS (1944–1951).

The data given hitherto have been taken from years in which the rains were typical, but the late dry season was rather mild. In order to show the extremes that may occur, additional records are given in Table III. These stream-bed records are based on the composite climate, i.e., Red Section pools in dry season, and White Section in rains.

Absolute temperature.—These are the most extreme figures ever recorded *on any day* during the six years of observations. Clearly, by settling *near ground-level* in the microclimate of the wet stream-bed, the fly can find cooler conditions on dangerously hot days; the general ecoclimate of the forest protects it from extreme cold, such as may occur in the woodland.

Mellanby (1936) found that for exposures lasting for three hours, 104° F. (40° C.) was fatal and 100·4° F. (38° C.) harmless at all humidities; but such results are rather misleading, as considerably lower temperatures are injurious, especially to the older flies. We have frequently noticed abnormally heavy mortalities amongst our stocks of tsetse after days on which the temperature reached 86° F. (30° C.) or over—an experience also suffered by Geigy (1948). This subject will be dealt with later, p. 132.

Maximum temperature and mean temperature.—These are the most extreme *mean monthly* figures ever recorded, and show that at seasons when the maximum temperature is abnormally high, a low resting position near water is advantageous to the fly, but not at cooler times of year. To a lesser extent this also applies to the mean temperature.

Saturation deficit and evaporation rate.—These are the most extreme *mean monthly* figures ever recorded, and suggest that striking advantages are to be obtained by tsetse in abnormal weather by resting near water near the ground. If the highest mean monthly readings are converted into terms of relative humidity, one gets the following results :

Woodland, 4 ft. : 24·0 mb. = 26 per cent. R.H. at 78·3° F. (25·8° C.).
Stream, 4 ft. : 20·4 mb. = 39 per cent. R.H. at 79° F. (26·1° C.).
Stream, 4 in. : 13·4 mb.= 50 per cent. R.H. at 72° F. (22·2° C.).

In Table II, which dealt with two of the milder years, there did not seem to be any striking advantage to the fly in settling near ground-level, but when the outside climatic conditions are abnormally severe, it would appear from Table III that whereas this severity is strongly reflected in the ecoclimate of the stream-bed at 4 ft., it is only slightly reflected in the microclimate at 4 in. At the lower height the stream banks should afford considerable additional protection from hot dry winds which are of sufficient force to penetrate the vegetational insulation and dissipate the damper air at 4 ft.

TABLE III.—*To show the extreme figures recorded for various meteorological readings during six years* (1944–1951).

	Open woodland.	Fringing forest stream-bed.	
	4 ft.	4 ft.	4 in.
Absolute temperature :			
Highest (° F.)	103·0	97·3	90·0
Lowest (° F.)	42·5	48·0	49·0
Mean monthly max. :			
Highest (° F.)	96·2	89·7	85·0
Lowest (° F.)	81·3	73·4	73·1
Mean monthly temperature :			
Highest (° F.)	83·3	80·0	77·9
Lowest (° F.)	70·2	65·1	64·3
Mean monthly evaporation rate :			
Highest (c.c.)	98	45	28
Lowest (c.c.)	5	1	0·5
Mean monthly saturation deficit :			
Highest (mbs.)	24·0	20·4	13·4
Lowest (mbs.)	0·0	0·9	0·0

However, a detailed, two-hourly analysis of the relative humidity of the stream-bed in March of a severe year has shown that the picture is not quite so simple as that just described. The relative humidity is lowest at both heights between 2 p.m. and 4 p.m., and highest between 2 a.m. and 6 a.m. On some afternoons, presumably when the wind is strong enough to dissipate even the microclimate, there is little difference in the lowest relative humidities recorded at the two heights ; on other afternoons the difference may be considerable. But the real advantage to the tsetse presented by the lower resting height is that here the *duration* of unfavourable conditions is greatly reduced.

For example, a week's analysis showed that whereas the diurnal period during which the relative humidity was below 40 per cent. averaged 9·3 hours per day at 4 ft., it averaged only 5·3 hours at 4 in.; similarly, the period during which the relative humidity was over 60 per cent. averaged only 0·5 hours per night at 4 ft., as against 4 hours at 4 in.

A very interesting point is that *the conditions in the microclimate remain remarkably constant irrespective of whether the season is exceptionally mild or unusually severe.* This is revealed by comparing the highest mean monthly figures recorded for 4 in. in Table II, based on the two mildest years, with those in Table III, which are the most severe monthly readings ever recorded in the 6 years, see below.

Factor. Mean monthly readings.	Microclimate. 4in. Table II (mild).	Microclimate. 4in. Table III (severe).	Ecoclimate. 4 ft. Table II (mild).	Ecoclimate. 4 ft. Table III (severe).
Max. temp.	82·0° F.	85·0° F.	86·0° F.	89·7° F.
Mean temp.	76·5° F.	77·9° F.	78·5° F.	80·0° F.
Evap. rate	23 c.c.	28 c.c.	28 c.c.	45 c.c.
Sat. deficit	12·0 mb.	13·4 mb.	15·3 mb.	20·4 mb.

If, however, we compare comparable figures for the ecoclimate at 4 ft., we find that the temperature is a little higher in the severe years, but that the evaporation rate and saturation deficit are much higher, indicating that in severe years the atmosphere of the ecoclimate becomes much drier. *N.B.*—Although the temperature increase is small, any increases at this level will be dangerous to the fly.

These results explain why, in the late dry season, *G. palpalis* is so often found only in those sections of thinly wooded streams where there are pools of water under well-defined banks. Such conditions, by providing a microclimate, afford an insurance against extremes of high temperature and prolonged exposure to low humidity; when these occur the tsetse has only to rest near the ground to assure survival of the species, even though longevity may be reduced by the killing off of old individuals.

Conclusions.

1. Although in mild dry seasons there is but little difference in the climate by the pools at 4 ft. and 4 in. above ground-level, in severe seasons it becomes apparent that there is a pronounced microclimate at the lower height.

2. Conditions in this microclimate remain remarkably constant irrespective of whether the season is exceptionally mild or unusually severe; but in severe seasons the atmosphere of the ecoclimate becomes much drier and the temperature rather higher, which is serious, as it enters the critical region.

3. Throughout the six years of observations, by utilising the microclimate, *G. palpalis* would never have had to withstand a temperature higher than 90° F. (32·2° C.), even though the temperature rose to 97° F. in the ecoclimate at 4 ft. and to 103° F. in the adjacent woodland.

4. As indicated by the *mean monthly* evaporation rate and saturation deficit figures of Table III, the humidity within the microclimate is far higher

than at 4 ft.; this is true over a period of 24 hours, and is due to the much shorter duration near ground-level of low, diurnal humidities, and to the longer duration of high, nocturnal humidities. However, it is suggested that the humid air of the microclimate can be *temporarily* dissipated by wind, because absolute relative humidities as low as 23 per cent. at 89° F. (S.D. = 35·6 mb.) have been recorded near ground-level, when readings at 4 ft. were 19 per cent. at 92° F.

5. The existence of this microclimate explains why in the late dry season the distribution of *G. palpalis* along thinly wooded streams is confined to pools of water under well-defined banks.

6. Throughout the six years of observations *G. palpalis* would never have had to withstand a temperature lower than 49° F. (9·4° C.); the general eco-climate of the fringing forest protects the fly from extremes such as may occur in the woodland.

5. CLIMATIC VARIATIONS IN THE SIX YEARS OF THE INVESTIGATION.

The climate of this area is usually fairly constant from year to year excepting for the latter part of the dry season, which in some years may be abnormally severe and prolonged, leading to considerable differences in the degree of survival of the fly population. It was not until we had worked out the order of severity for the six years that the meaning of our fly data became plain.

In fig. 3 climatographs are shown for the six years, being based on mean monthly maximum shade temperature and mean monthly evaporation measured at 4 ft. height in the White Section. It will be remembered that in this section the stream dries up, and in severe years the section may be evacuated by fly.

The dotted lines, showing the intersection of 90° F. and 40 c.c., are intended as a guide to the eye; when months fall outside these lines in the late dry season, the climate may be taken as being unusually severe.

The climatographs should be read by starting at November, the eleventh month, which marks the commencement of the dry season, and reading round until the following October. (*N.B.*—The first year's readings did not start until December.) Since a biological year has been adopted in preference to a calendar, the successive years will be referred to in the text as 1st, 2nd, 3rd, etc., rather than 1944–'45, 1945–'46, 1946–'47, etc.

The cold season—November to January—usually consists of rather hot days but very cold nights, and is therefore more readily discernible by studying the minimum or mean temperature. Hence, in fig. 3, where maximum temperatures are used, the cold season is masked except in December of the 2nd and 3rd years, when heavy Harmattan haze obscured the sun and lowered the maximum temperature.

Conditions in the late dry season were quite exceptional in the 1st year with three consecutive months falling outside the dotted lines; the evaporation rate was abnormally high. In the 2nd year the maximum temperature was above average for two months, but the evaporation was not excessive. The 3rd, 4th and 5th years were less severe, the 4th year being exceptionally cool. The 6th year is the second most severe, but even so it cannot compare in aridity with the 1st year, as the evaporation rate was far less. It is significant that in

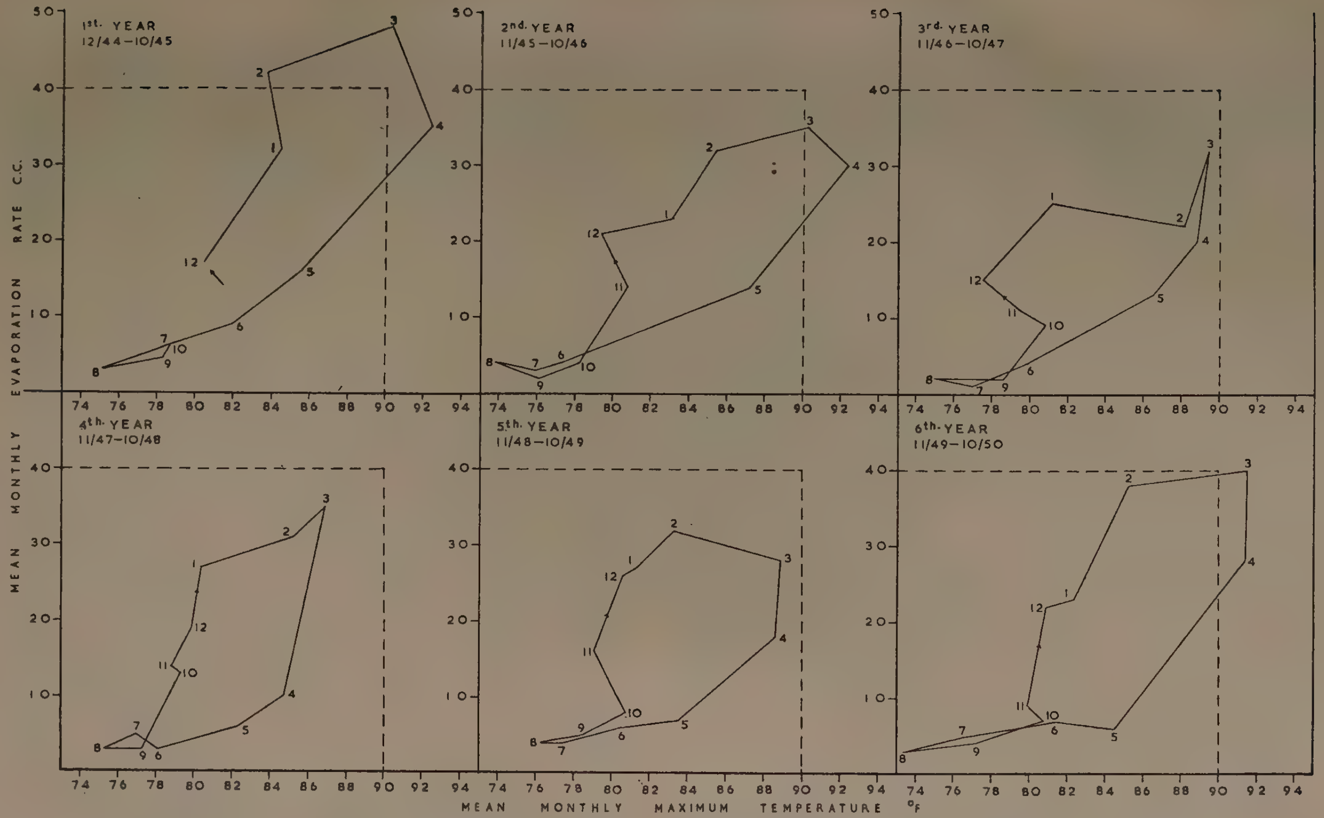

FIG. 3.—Climatic variations during almost six years of the investigation, illustrated by climatographs for each year. (Based on mean monthly evaporation rate and maximum temperature.)

the 1st and 6th years the dry season was prolonged, there being no rain until the second half of April. If the late dry seasons are placed in descending order of severity the years could be arranged as follows: 1st, 6th, 2nd, 3rd and 5th, 4th.

It should be noted that the fourth month, April, is climatically most variable, depending upon whether the rains are early or late, cf. April of the 1st and 4th years on fig. 3.

In the heavy rains climatic conditions from July to September inclusive are most constant throughout the years, with the evaporation rate ranging from 5 to 10 c.c. and the mean maximum temperature from 74° to 79° F.

* * * *

It has been shown that in late dry seasons of abnormal severity such severity is strongly reflected in the fringing forest ecoclimate at 4 ft., but only very slightly in the stream-bed microclimate near water at 4 in. In such years this microclimate, which is dependent on water, may be essential to fly survival in reaches of a stream where the vegetational insulation is inadequate.

For this reason the presence or absence of water in the stream-bed has always been recorded on fly-round days for all the subsections that form a colour section. The number of months in each year in which a colour section was dry for its whole length is recorded in Table IV. When deciding whether the late dry season conditions as experienced by the tsetse were exceptionally severe in any particular year, it is considered necessary to consult Table IV as well as the climatographs in fig. 3.

TABLE IV.—*The number of months in each year in which the stream-bed was dry in* all *subsections of each colour section.*

		Main fly-round.				Total rainfall of *preceding* wet season (inches).
Year.	Green.	Red.	White.	Blue.	Yellow.	
1st . . .	?	0	5	5	4	39·0 approx.*
2nd . . .	2	0	3	4	4	49·2
3rd . . .	2	0	1	1	2	48·4
4th . . .	0	0	0	1	1	48·9
5th . . .	1	0	0	1	1	50·6
6th . . .	2	0	3	3	3	41·2

* Rainfall records not yet started at Katabu, but only 39·4 in. precipitated at airport 12 miles away. Other stations to north and south were 10·4 and 11·4 in. below average.

Table IV shows that whereas in six years the Red Section was never entirely dry, all the other sections dried up in certain years. White, Blue, and Yellow sections are all drier than Green.

The climatographs, fig. 3, suggested the following descending order of severity for the late dry seasons of the six years: 1st, 6th, 2nd, 3rd and 5th, 4th. But Table IV suggests the following order: 1st, 2nd, 6th, 3rd, 5th and 4th.

We can conclude, having taken into account both fig. 3 and Table IV, that the 1st year was the most severe and the 4th year the mildest, and that the correct descending order of severity should be: 1st, 2nd and 6th equal, 3rd, 5th, 4th.

The rainfall of the preceding year has been recorded in Table IV because it is believed that the extensiveness of the microclimate depends more upon the height of the water table, and therefore upon the rainfall of the previous year or years, than on the climate experienced at the time. The rainfall immediately preceding the 1st year's dry season was probably some 10 in. below average, and that which preceded the 6th year was 8 in. below the average for the four previous years at Katabu; in these two years the stream was very dry, especially in the 1st year. The dryness of the 2nd year probably reflects a water table that was still very low as a result of the very poor rains which preceded the 1st year, whereas the relative abundance of water in the stream in the 3rd, 4th and 5th years was probably due to a succession of years of good rainfall.

Conclusions.

1. The severity of the late dry season climate cannot be assessed solely by the meteorological records obtained at the time. Since *G. palpalis* depends at this season upon the *extensiveness* of the microclimate, it is also necessary to record the degree to which the stream has dried up.

2. After taking both sets of records into consideration, it was decided that the dry seasons of the six years investigated should be placed in the following descending order of severity: 1st, 2nd and 6th equal, 3rd, 5th, 4th.

The extent of the microclimate at the end of the dry season is believed to be largely dependent on the height of the water table, and therefore upon the rainfall of the preceding year or years.

6. FLY CONCENTRATION AND DISPERSAL IN RELATION TO SEASON.

(a) The Seasonal Distribution of Marked Flies on the Whole Fly-round.

Throughout the investigation the site of recapture of each marked fly has been plotted monthly, in colour, on scale diagrams of the fly-round. Unfortunately it is quite impracticable to publish these charts for 72 months, but samples are shown in fig. 4. The stream is represented diagrammatically, but to scale, by the horizontal columns; the presence of water in the stream-bed is denoted by hatching. Recaptured marked flies are indicated at the site of their recapture by letters denoting their section of origin, i.e., R = Red, B = Blue, etc.; thus an " R " at Yellow Section denotes a fly that must have travelled from Red. All " stranger " marked flies that have come in from other sections are recorded *above* the horizontal column, whereas all " residents," or flies recaptured in the section in which they were originally marked, are recorded *below* it.

In fig. 4 comparisons can be made between the marked fly distribution in the driest and hottest month of March and in the wettest month of August—*and* in two very different years. The 1st and 4th years have been selected because they demonstrate distribution in the most and least severe dry seasons of the investigation. Hence the reader can study the distribution at opposite times of year and in opposite types of year, and can visualise the gradations that link these extremes.

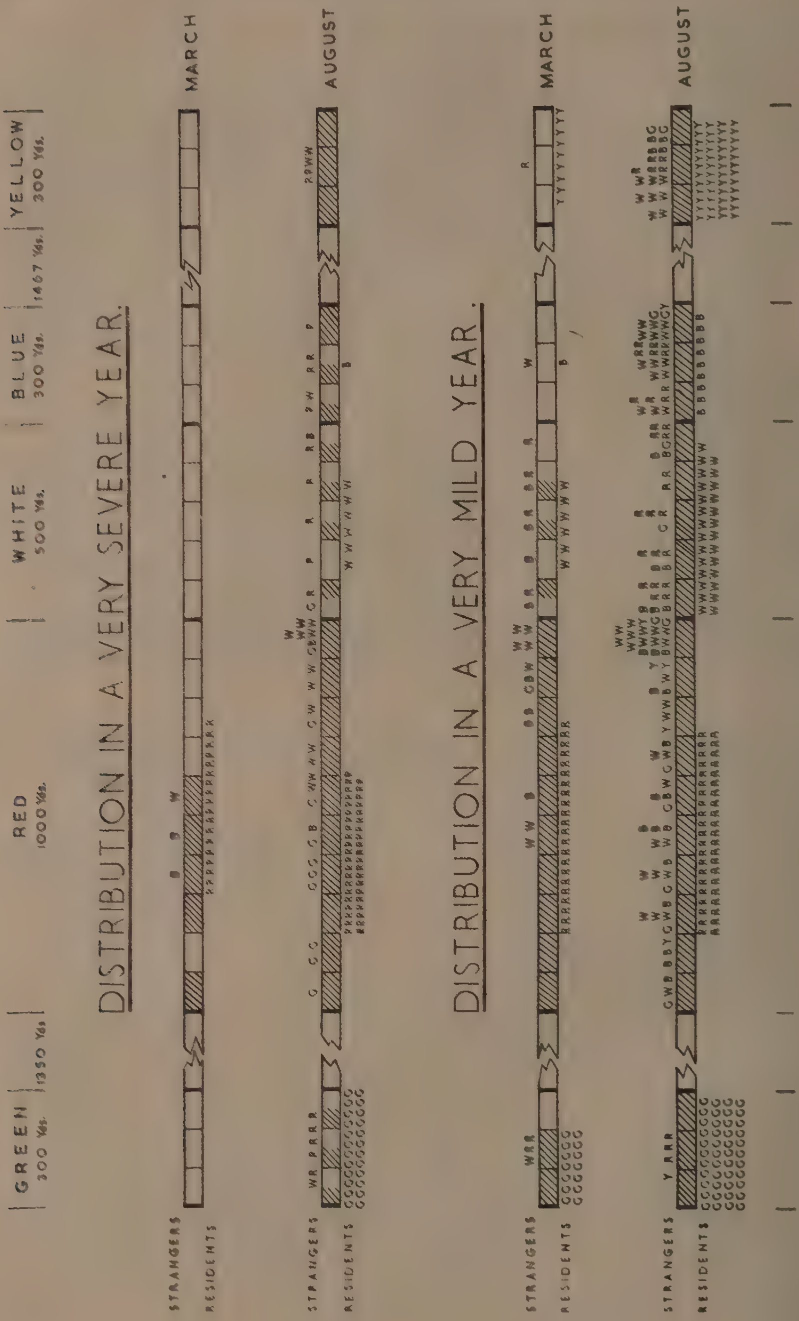

Fig. 4.—The seasonal distribution of marked flies on the fly-round.

1st Year.—Very Severe.

By March of the 1st year, when a record high evaporation rate occurred, the whole stream had already been dry for 2 or 3 months except for Red Section, where there were still pools of water. It is significant that not a single marked fly was found in the dry White, Blue and Yellow Sections, but that the survivors were all located in Red; most of these were residents. This focus persisted in Red until the following June (not shown), when Red flies entered the White Section. (*N.B.*—Green Section had not been started by March.)

By the following August recolonisation of the stream had taken place, and it will be seen that the picture had become entirely different: the stream had not yet started to flow continuously, but water was abundant and the climate typical for the heavy rains. The fly population had increased greatly, and flies were wandering up and down the length of the stream, e.g., Red flies were found in both Green and Yellow, those in the latter section having travelled over 1¼ miles. Green flies had got as far as the White Section, and White flies had reached Green. This state of affairs continued until December (not shown), by which time a Yellow fly had reached the Green Section, having travelled 2¾ miles.

4th Year.—Very Mild.

By March of the 4th year, which was unusually cool with a relatively low evaporation rate, the Blue and Yellow Sections had just become dry but remained so for this one month only, instead of for a total of 5 and 4 months respectively, as in the 1st year, cf. Table IV. The March picture was more like August, with an abundance of stranger flies—Red flies in Green and Yellow and a Green fly in Red. Clearly, there was no concentration in Red, and travel never really ceased. Admittedly, fly numbers were low as compared with August, but this is always the case at this time of year, as will be shown later.

By August, the basic picture was unaltered except that flies were far more numerous. Unlike August of the 1st year the stream was running continuously, and travel was on a greater scale—Green flies being taken in Yellow and Yellow in Green.

A study of the original coloured charts suggests that in the early dry season of most years there is a build up of Yellow flies in Red or adjacent White, and a build up of White and Blue flies in Red, near its junction with White. The picture suggests that as the down-stream sections dry up the flies tend to move towards, and into, Red. If such an up-stream movement does take place, it is not suggested that flies know whether to move up-stream or down-stream but rather that the flies, by settling near water, tend to get drawn up-stream as the stream dries up towards Red.

(b) The Season of Long Travel.

Since the number of marked flies recaptured is very small at certain seasons, it has been found necessary to group by months all the data collected over 6 years. As an arbitrary means of indicating "long-travel," we have recorded separately all those individuals which are known to have traversed *at least* 1000 yards from the colour section in which they were originally marked;

the bulk of these will have travelled a considerably greater distance because the length travelled has been measured from the end of the colour section nearest to the point of recapture, whereas the fly may have been originally caught and marked at the opposite end of that same colour section. The data are shown in Table V, where the recaptures which are known to have travelled over 1000 yards are expressed as a percentage of the total recaptures for that month.

TABLE V.—*The season of long travel.*

(Out of the total marked flies recaptured in each month over six years, the monthly percentage which had travelled over 1000 yards, or 914 metres.)

	The dry season.					The wet season.						
	Early dry, or cold season.			Late dry, or hot season.		Early rains.		Heavy rains.				End of rains
Months :—	XI.	XII.	I.	II.	III.	IV.	V.	VI.	VII.	VIII.	IX.	X.
Total marked flies recaptured	672	622	320	232	363	412	468	383	578	874	966	891
Percentage of recaptures that had travelled over 1000 yds.	18	22	21	16	5	6	8	16	23	21	25	31

Considerable travel takes place throughout the cold, early dry season, but decreases at the start of the hot weather in February and is minimal in the hot months of March, April and May ; whereas March is a hot, dry month, April and May are hot, but relatively humid months. Travel starts again at the beginning of the heavy rains, and becomes maximal in October when the rains are ending.

It is interesting to note that the great reduction of travel appears to be associated with high temperature and not humidity. Jack and Williams (1937) showed by laboratory experiments with *G. morsitans* that at normal temperatures this species gives a positive reaction to light, but that if the temperature is raised sufficiently the reaction of the flies is reversed and becomes strongly negative.

If *G. palpalis* behaves in the same way as *G. morsitans*, it is probable that for many hours of the day in the hot weather the negative reaction to light will be operative, and will therefore confine the fly to the darkest and densest vegetation, where vegetational insulation is good ; but when, in cooler weather, the positive reaction to light is operative, the tsetse will fly readily along the edge of the fringing forest, cut across small bends in the stream, and so transverse long distances. If this explanation is correct, it would account for the considerable lag that takes places between the beginning of the rains and the re-colonisation of the evacuated sections.

It is suggested that a negative reaction to light at high temperature may account for the tsetse's seasonal avoidance of those parts of its environment which, owing to high temperature and low humidity, would prove to be temporarily injurious, if not lethal. There may also be a positive reaction to humidity which becomes operative when the atmosphere becomes too dry and so attracts *G. palpalis* to the presence of water, but there is no evidence for this.

The longest distance recorded for travel by a marked fly was just over 3 miles (5 kilometres) ; this tsetse had travelled from Yellow Section, up-stream, to a point between Green and the source. On a narrow stream of the type investigated, in which low creeper-tangles are common and the fringing forest meets overhead, we doubt whether *G. palpalis* often travels more than 2 miles from its birthplace during its life-time: the covering of appreciable distances is probably dependent upon climatic conditions permitting the fly to make unobstructed flights along the outside edge of the fringing forest. On wider watercourses flight is easy along the shaded river-bed and probably much greater distances are traversed.

On the Bahago stream flies have frequently been recaptured which must have travelled 1000 yards within 24 hours of marking, and 2000 yards is not uncommon; the record for one day is 3250 yards, or just under 2 miles.

Two marked *G. palpalis* from the Bahago have been recaptured in another stream the other side of the watershed. One of these had been marked in the Red Section and, even if it had followed up-stream and passed Green to the source, it would still have had to cross just over one mile of woodland to reach the other stream. These flies may of course have been carried by man, but such incidents do show that in any effort to eradicate *G. palpalis* by measures other than clearing, one has to guard against re-infestation from nearby streams even though they belong to another system.

Long-travel is not confined to any one sex. Thus, during the first four years, out of 712 flies that had travelled at least 1000 yards, 54 per cent. were females.

(c) A Study of Fly Concentration and Dispersal on the Main Fly-Round.

It is believed that the Red Section, with its very narrow fringe of forest, would never be especially attractive to *G. palpalis* were it not for the presence of pools of water in the late dry season—a time when the other sections are dry. This fact becomes apparent when studying the coloured charts referred to in the last section; an endeavour has been made in fig. 5 to present some of these data in a form less abhorrent to an editor.

Data have been taken for flies marked and recaptured on the main fly-round only, i.e., Red, White and Blue Sections, which total 1800 yards in length. The results are expressed as the percentage of the total recaptures on the main fly-round occurring in the Red Section. Since the Red Section occupies 1000 out of the 1800 yards, on a purely linear basis one would expect 56 per cent. of the recaptures to occur in Red; a line has been ruled across fig. 5 for this percentage. Theoretically, when the percentage of the total recaptures taken in Red is above 56 per cent., then Red is more attractive than the other two sections combined.

Out of the total number of wet subsections found on the main fly-round, the percentage occurring in the Red Section is shown in fig. 5 by columns: when the columns register 100 per cent., then obviously White and Blue are completely dry. Hence, should marked flies be especially attracted to the Red Section at any season, it will become evident whether or not this attractiveness is associated with the presence of water, upon which the microclimate depends.

The years are written across the top of fig. 5, and the relative severity of their dry seasons, as finally decided on p. 91, is indicated by the letter A, B, C, D, and E; A is the most severe and E the least. The 6th year is not shown because the numbers of marked flies recaptured were unfortunately too small to allow of their being expressed as percentages.

Fig. 5 shows that the seasonal attractiveness of the Red Section follows a very definite annual cycle—pronounced in the years with severe late dry seasons, but perceptible even in the mildest year. The cycle consists of two parts, the concentration period when the drying up of the pools elsewhere leads to Red becoming progressively more attractive—December or January to March, April or even May—followed by the dispersal period, which starts when water reappears in the other sections and continues throughout the rains into the following early dry season—November or December.

The concentration period.—In the 1st and most severe year, poor rains lead to an early onset of severe climatic conditions and to an early concentration in Red. For four months—January to April—water was to be found only in Red, and for four months—February to May—100 per cent. of the marked flies were found in this section, suggesting complete concentration. The lag between the drying up of the stream in White and Blue and peak concentration in Red is probably due to the continuation of wet mud in the stream-bed after the pools were recorded as waterless.

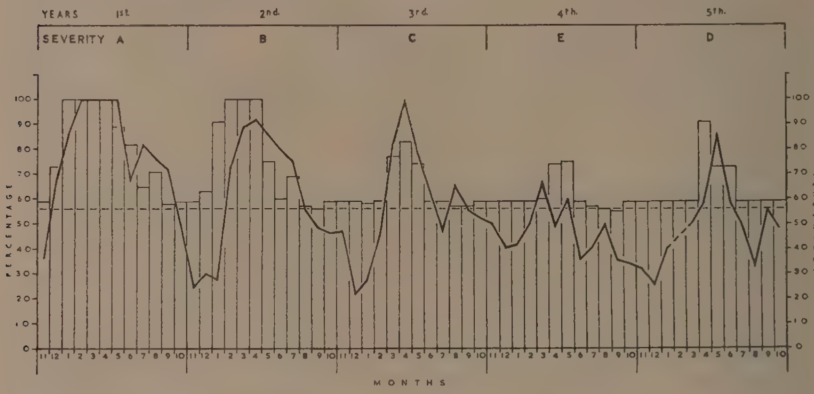

Fig. 5.—Variations in the seasonal attractiveness of the Red Section, year by year.

[Out of the total number of flies marked and recaptured on the main fly-round, the percentage found in Red Section (line); also, out of the total number of wet sub-sections found on the main fly-round, the percentage found in Red Section (columns).]

In the rather less severe 2nd year White and Blue were waterless for a month less, and concentration was not quite complete and lasted for a shorter time. In the much milder 3rd year there was only a brief period of concentration.

In the 4th, the mildest year of the investigation, concentration was barely perceptible, whereas in the 5th year, when conditions were a little more severe than in the 4th, there was a definite brief period of concentration.

The dispersal period.—After severe late dry seasons dispersal is slow, and Red becomes relatively unattractive for only 4 to 6 months of the year (as indicated by the curve falling below the 56 per cent. line); but after the mild dry season of the 4th year Red was relatively unattractive for 10 consecutive months. Indeed, during the 18 months from September of the 3rd year until March of the 5th year the curve was only twice above the 56 per cent. line.

It may be concluded that the Red Section, with its very narrow fringing forest, is unattractive except in severe late dry seasons, when its pools make it vitally important as a survival focus, from which the adjacent reaches of the stream can later be repopulated.

* * * * *

Hitherto we have dealt with marked flies only. It may be argued that we have only shown that Red represents a reach of stream whose flies will survive severe seasons, when the flies of other sections succumb, and not that flies from other sections tend to move into Red and so produce a concentration.

If we study the actual fly density consisting of both marked and unmarked flies, it will be found that in the most severe years the number of flies in Red is abnormally great, which suggests that the population must have been increased by flies moving in from outside. Were this not the case, one would expect that in such years the severe climate would lead to a lowering of density in Red associated with the virtual extermination of flies in White and Blue.

TABLE VI.—*Yearly variations in the degree of fly concentration recorded near the permanent pools of the Red Section.*

(Fly density for the month of March in each of the six years, expressed as flies per boy per 100 yards.)

Sections.	Severe. 1st year.	2nd and 6th years.		3rd year.	5th year.	Mild. 4th year.
Red	1·60	0·87	0·73	0·27	0·14	0·51
White	0·10	0·28	0·50	0·35	0·53	0·80
Blue	0·04	0·13	0·04	0·21	0·21	0·38

In Table VI density is expressed as flies per boy per 100 yards; densities are given for the month of March for the six years, which have been arranged in descending order of severity. The results suggest that a certain proportion of the population from other parts of the stream must find its way into Red, and thus account for the abnormally high population found there in the most severe years.

When studying the table it should be remembered that White is contiguous to Red, so that if a few flies which are really resident in Red are caught when seeking food in adjacent White, their capture will tend to mask the degree of evacuation that has really taken place from White; for this reason a comparison of the densities in Red and Blue gives the better picture.

Reading the columns downwards, in the 1st and most severe year, White and Blue were virtually evacuated: 130 flies were caught in Red, as compared with 4 in White and 1 in Blue. In the 2nd and 6th years the same tendency for the bulk of flies to be taken in Red is observable but on a decreasing scale, as these dry seasons were less severe. In the three mild years, 3rd, 5th and 4th, the picture is reversed, the density being higher in White than in Red. A comparison of the densities of Red and Blue throughout the years shows that as the seasons decline in severity, so the density of Red decreases from having been 40 times greater than Blue in the 1st year until it is less than that of Blue in the 5th year. (Admittedly this trend broke down in the exceptionally mild 4th year, when Red was more attractive than might have been expected.) If the columns are read from left to right, it is clear that whilst the trend is for the density of Red to decrease steadily with seasons of decreasing severity (with the exception of the 4th year just referred to), the trend is for the densities of White and Blue to increase as the years become milder.

It may be concluded that under conditions most inimical to fly survival the density of Red increases because its population is swollen by some of the flies from the adjacent sections, i.e., real concentration takes place.

* * * * *

(d) The Economic Implications of the Findings to Date.

The permanent pools of the Red Section typify the sort of place where man sites his village ; let us suppose that there is a village there. It has been shown that after a poor wet season in which the rainfall is considerably below average, the stream tends to dry up rapidly and the surviving tsetse population concentrates in the reach where there are permanent pools. For three or four months the tsetse are confined to this small area, being unable to leave the microclimate for long. The natives are also dependent on these pools for their water ; even if they have shallow wells in the village, these will almost certainly be dry in such a year. The tsetse will be feeding almost entirely on man, because no game will venture so close to habitation. Under such circumstances a close, personal man-fly contact is brought about. If one of the villagers has transmissible trypanosomes in his blood-stream, the tsetse may become infected and transmit the disease to other villagers. Some time after the rains have broken these tsetse will start to recolonise the stream, and an infected fly may travel to another hamlet one or two miles further along the stream and introduce the disease there. The effects of this abnormally low rainfall may have lowered the water table for the next year or two, and so permit these conditions to be reproduced during two or three consecutive seasons, but to a diminishing extent.

It has been shown that after a succession of good rains the water table rises and *G. palpalis* tend to remain dispersed along the stream, and to travel widely. This leads to the much less dangerous type of impersonal man-fly contact in which the fly, having had, say, one meal on a man near the village, has its next on an antelope possibly a mile further down the stream. But such years, when the water table is high and there is no fly concentration, are probably particularly bad for the spread of bovine trypanosomiasis.

In Northern Nigeria the bulk of the cattle population is owned by the nomadic Fulani, who tend to spend the rains in the tsetse-free north, and in the dry season to move southwards into fly country in search of grazing. After the bush fires the best grazing is to be found along the valley bottoms, where new grass shoots up within a few weeks of the fires. In mild years when fly remain dispersed along hundreds of miles of stream the risk to the cattle must be far greater than when tsetse are confined to the immediate vicinity of water-holes. It is believed that these remarks are equally applicable to that other riverine tsetse, *G. tachinoides*. Nash (1937) found that the longer the rains lasted the greater the degree of dispersal achieved by *G. morsitans*; when dispersal is exceptional the Fulani are likely to lead their cattle through areas which are normally safe, and not realise their mistake until too late.

The observations on *G. palpalis* which have been described above suggest:

1. After a season of abnormally low rainfall there may be an increase in the incidence of human sleeping sickness, which may continue with decreasing intensity for one or two years until the water table is replenished.
2. After a season of abnormally heavy rainfall or after a succession of years of good rainfall there may be an increase in bovine trypanosomiasis, which may continue until the water table is lowered.

There is no reliable epidemiological evidence to support these hypotheses. In regard to human trypanosomiasis, any long-term cycle in the incidence of the disease is nowadays masked by periodic mass treatments, while no adequate data are available for bovine trypanosomiasis.

7. FLY DENSITY AS RELATED TO SEASON.

Density data have been taken from the main fly-round only, because it includes nearly equal lengths of contiguous fly concentration and dispersal reaches of the stream. The fly density is expressed as flies per boy per 100 yards (F.B.100Y)

Fig. 6 shows the rainfall by half months, the mean monthly evaporation rate at 4 ft. in the White Section, and the mean monthly fly density and females per cent. At the bottom, the years are shown and the relative severity of their dry seasons are again indicated by letters—'A' being the most severe and 'E' the least.

(a) Seasonal Fluctuations in Fly Density.

In order to understand the annual cycle for seasonal fluctuations in fly density, the reader should ignore temporarily the 2nd and 3rd years when fly density was abnormally low, and study the graph from April of the 4th year until April of the 6th year. The cycle appears to fall into two parts. Firstly, in each year, there is the wet season period of increase, with fly density rising rapidly from April to September, following upon a falling evaporation rate. Secondly, there is a long period of general decrease throughout the dry season (October to March), which, at first sight, appears to be entirely associated with rising evaporation rate. Actually, the picture for this second part is not quite so simple as it seems.

The fall in density which usually occurs in October, the last month of the rains, is *not* associated with rising evaporation rate, but is due to the almost saturated atmosphere of the preceding months when the evaporation rate became too low. This is readily discernible in the 1st year when the peak density was early, occurring in August, and the fall started in September, *when there was heavy rain and the evaporation rate was almost minimal.* The ill-effects due to the evaporation rate having become too low are so transitory and are so rapidly followed by a soaring evaporation rate which becomes too high that the fly density appears to fall more or less continuously; however, it will be noted that there is a tendency for the fall to check about December, which may be partly due to the brief October-November period when the rising evaporation

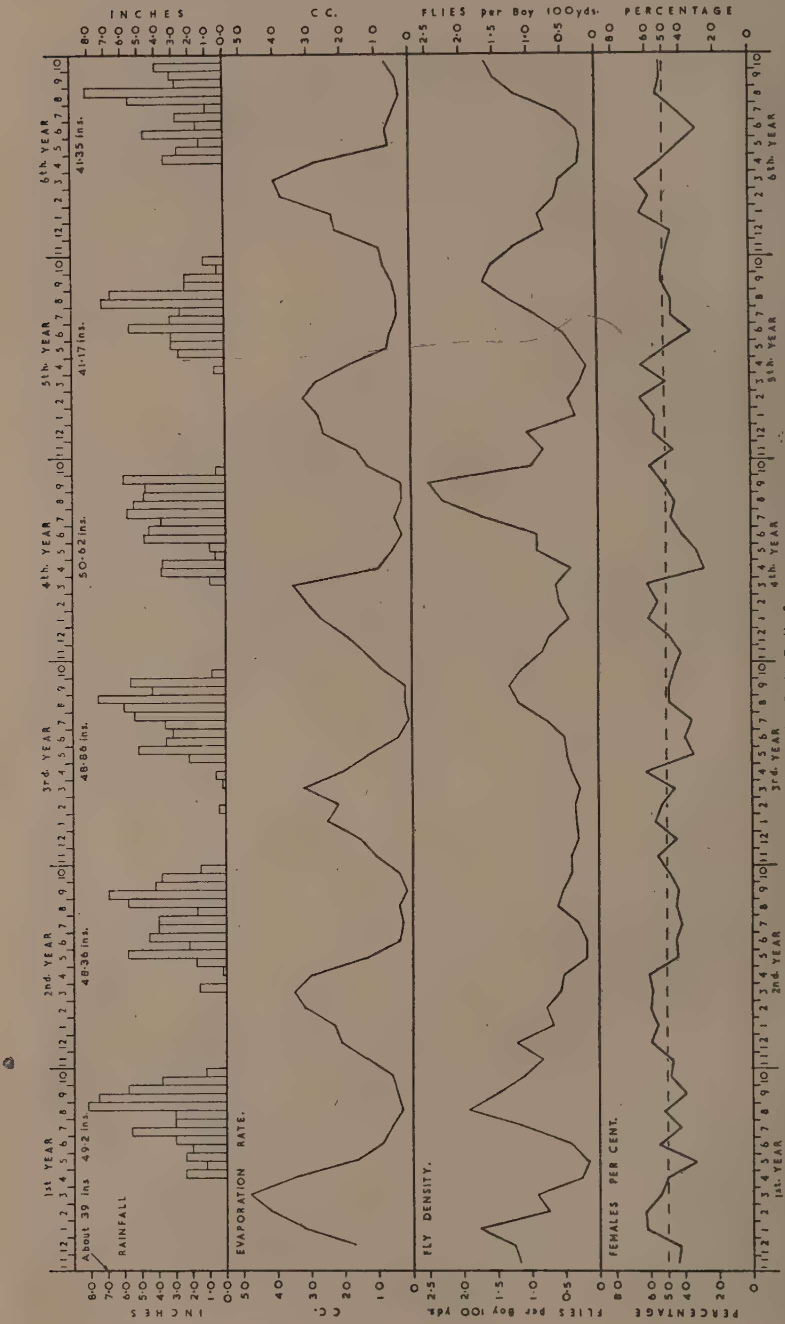

FIG. 6.—Seasonal fluctuations in monthly fly density and females per cent., over 6 years.

rate is rapidly passing through a favourable, median level, and partly due to fly concentration, as will be described shortly.

The control fly-round at Jaji gave very similar seasonal fluctuations to those just described.

This mainly inverse relationship between the evaporation rate and the density of *G. palpalis* is very similar to that found for *G. morsitans* in Northern Nigeria (Nash, 1937, p. 98, lower half of fig. 5), although of course the optimum zone of evaporation for *G. palpalis* is considerably lower, being around 8 c.c. instead of 20–25 c.c.

Reverting again to fig. 6, in December of the 5th year and January of the 6th year there was a check to the falling density of the early dry season. This halt, or even rise in density, is believed to signify the entry into the main fly-round of stranger tsetse from the reaches below Blue Section which are drying up. In the 1st year, when concentration was far greater than in any other year (fig. 5), the checks referred to took the form of abrupt rises in density in January and March ; in the 2nd and 5th years these rises occurred in December and February ; in the 4th, or mildest year, these checks were barely perceptible. (The reader may wonder why the checks were so small in the 6th year, remembering that this was described as the second equally most severe season. The reason probably was that by the 6th year, the Yellow Section, as a result of fire exclusion, was no longer being completely evacuated by flies as in the earlier years ; many of the flies which would normally have moved up to the main fly-round, *en route* for Red, were probably now remaining in Yellow. This will be dealt with under vegetation, p. 146).

If the explanation for these temporary checks or rises in the dry season is accepted, it will be seen that the cycle described for the last two years is apparent in all the years. However, some great disaster befell the tsetse population in the early rains of the 2nd year—a disaster which prevented the usual increase of the fly population from its low level in May to its very high level in August or September. The late dry season had not been nearly so severe as in the 1st year, and the population surviving in April was accordingly much higher and should have permitted a rapid increase in the population during the ensuing rains. The normal trend for a rise between June and August is present, but the degree of rise is negligible.

A similar disaster befell the tsetse population on the Jaji control fly-round which is ten miles away, so that it cannot have been due to any purely local cause such as the disappearance of game. The meteorological records have been studied with the greatest care, and the only unusual features were several quite abnormal deluges in the late dry season and early rains, which brought the stream down in spate much sooner than usual.

On 18th March, 1946, 1·7 in. of rain fell most unexpectedly and washed away all the stream-bed instruments and presumably all the tsetse pupae as well. In no other March has such a happening ever been recorded ; the average rainfall for this month during the other five years is only 0·24 in. The important point is that this freak storm occurred at the hottest and driest time of year, when the surviving tsetse population was concentrated by the pools and was breeding in the stream-bed. The ill-effects of this storm were not apparent in April as it would not have affected the adults, but when these started to die off and were not replaced by young flies the density for May dropped to one-third of what it had been in April: in no other year did the May density drop appreciably below that of April. For May and June the fly density was only 0·17 F.B.100Y.

Recovery from the ill-effects of the storm may have been further hindered by the absence of rain during the next six weeks, the weather remaining very hot and dry, and still further by a second storm on May 25th that was unusually heavy for the time of year, 2·3 in. being precipitated and the stream banks flooded. Rainfall at Jaji was only measured every other day, but it is clear that both these storms occurred there.

Heavy precipitations of 2 in. or over are common in the heavy rains, but by that time the evaporation is low and *G. palpalis* is believed to have less restricted breeding habits, as will be described in the next section. We are suggesting that a great destruction of puparia is only likely under the abnormal conditions provided by an unexpected deluge occurring when a very high evaporation rate is enforcing concentration by the pools.

These freak conditions appear to have so reduced both the survival stock of *G. palpalis* and the recovery period before the start of the next dry season that the fly community was quite incapable of building up adequate numbers in the time remaining. In consequence this process had to be postponed for a year until the favourable season for recovery came round again.

This recovery season would appear from the graphs to extend from May or June until August or September, but in fact starts in April, when the expectation of adult life is greatest; this will be gone into later. In this season the population may increase up to thirteen-fold in 3 months, (see 1st year).

There is also a reduction season, October to April or May. In the 4th and 5th years the population decreased to one-fifteenth of its original density in 7 months; and two-fifths of this decrease occurred in the one month, September to October. The reduction rate is much slower than the recovery rate. This subject will be dealt with in detail, pp. 135–139, after relevant data on seasonal longevity and the reproduction rate have been given.

(b) Seasonal Fluctuation in the Sex Ratio.

Out of 17,306 *G. palpalis* caught over 6 years on the fly-round, 49·1 per cent. were females. Out of 1903 flies bred from pupae, 52·4 per cent. were females. There seems therefore no reason to suppose that the females of *G. palpalis* are reluctant to appear to man, since they are recaptured in almost equal number with males. Throughout West Africa the females per cent. usually ranges from 40 to 50 (Nash, 1948*a*, p. 74).[1]

On fig. 6 the females per cent. has been plotted for 6 years. As a guide to the eye a dotted line has been drawn along the 50 per cent. line. There is a definite tendency for the females per cent. curve to be above 50 per cent. in the dry season, particularly in January, February and March when the evaporation rate is highest. Further, in every year there is a sharp fall in the early rains from a percentage that is often nearly maximal to one that is minimal;

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[1] Squire (1952) explains the low female per cent. at Njala, Sierra Leone, on the grounds that females avoid copulation when pregnant, and so are less active; this explanation is not admissible in our area, nor in the many other parts of West Africa, where the sexes are equally active.

this fall is associated with a great decrease in the evaporation rate ; in the 4th year the females per cent. figure fell from 62 in March to 27 in April.

It is very hard to find an explanation for these facts, but the relationship between the evaporation rate and the females per cent. suggests that the appearance of females in larger numbers in the dry season might be associated with the hunger cycle. One could postulate that in very dry air gravid females have to take food more often than males and that therefore they appear in greater numbers, whereas in the rains, when the hunger cycle is much longer, the males are commonest, not because they feed more often, but because they have to search for the females, which are inactive at this season for much longer periods. There is no evidence for this postulate, but it is the only one we can think of which would fit the facts.

(c) The Economic Implications of the Results.

The findings described above are believed to have considerable economic implications in those vast areas of the West African savannah zone which have a definite dry season of four months' duration or longer. On ecological grounds attempts to destroy *G. palpalis* by various measures should be timed to start at the outbreak of the rains when the tsetse population is lowest, and should be continued throughout the recovery season until the end of the rains. Should any flies survive, these will now have to face the natural season of reduction with no hope of increasing their numbers until the recovery season comes round again.[2]

8. FLY-BREEDING AS RELATED TO SEASON.

The subject of seasonal fluctuations in breeding by *G. palpalis* is exceedingly complex ; difficulty has been experienced in elucidating the problem, despite the use of different methods of approach.

(a) Results from Searching for Puparia.

Throughout the six years, on the 1st and 2nd days of each month, half-hour searches were made in each subsection of the main fly-round by six highly skilled men. They examined all the classical sites such as beneath logs and leaning trees, the humus of the forest floor, the soil of the stream-bed, hollows in trees, etc.

The results, expressed as puparia per boy hour (P.B.H.), are shown in fig. 7 ; they suggest that annually breeding starts at the beginning of the dry season and reaches a peak about December ; it would then appear that usually breeding decreases rapidly and ceases in May, at the end of the early rains. But this is obviously fallacious, because it has been shown that the fly population increases enormously throughout the rains, which would be quite impossible if breeding ceased in that season.

The correct interpretation of fig. 7 is believed to be as follows : In the early dry season the searchers start to find puparia in ever-increasing numbers as the soil becomes drier, which makes searching much easier. Their work is also greatly facilitated by the fact that as the climatic conditions become more severe, breeding shifts in towards the stream-bed and becomes concentrated in relatively few well-protected sites; this gives the illusion of a great increase in breeding. On the other hand, the late dry season decrease in pupal density is believed to be genuine, as it is related to the great decrease in adult density which characterises that season. The apparent absence of puparia in the rains will be discussed shortly.

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[2] A recent report by the Colonial Insecticide Research Unit has just been received, describing their first apparent success in eradicating tsetse (*G. swynnertoni*). It is noteworthy that on this occasion they sprayed the vegetation when the fly population was minimal and continued into the recovery season (C.I.R., V, 24.vi.52).

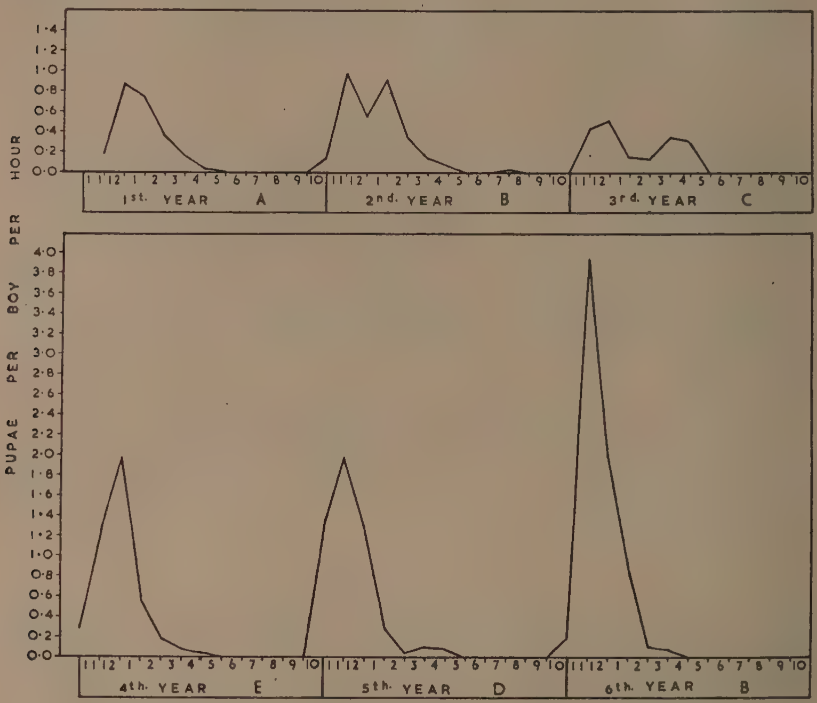

Fig. 7.—Seasonal fluctuations in the pupal density of the classical sites, over 6 years.

Once the limitations of fig. 7 are appreciated, it becomes worthy of further study. The great variation in the numbers of puparia found in December of each year tends to be associated with the size of the fly population at the end of the rains. For instance if we take the fly density for the latter half of October and compare it with the pupal density at the beginning of December, we find that in the 3rd year a fly density of only 0·42 F.B.100Y gave rise 5 weeks later to a pupal density of only 0·44 P.B.H., whereas in the 2nd year 1·10 F.B.100Y gave rise to 0·98 P.B.H., and in the 6th year 1·55 F.B.100Y gave rise to 3·94 P.B.H.

In the 5th year pupal density was abnormally high for November, but in that year the rains ended very early.

It was mentioned before that the December check in the falling fly density of the 2nd year was believed to be due to an influx of stranger flies seeking sanctuary in the main fly-round; this check is reflected in the pupal density which increased in early February, instead of continuing to fall. The figures are:

1·10 F.B.100Y for late October, gave 0·98 P.B.H. in early December.
0·84 ,, ,, November, ,, 0·57 ,, ,, January.
1·23 ,, ,, December, ,, 0·95 ,, ,, February.

The unusual curve of the 3rd year may be associated with an unusual fall of rain in early February.

Owing to the small number of puparia found in the late dry season, it is impossible to show that the yearly variations in the degree of pupal concentration agree with the yearly variations in the degree of adult concentration as shown in fig. 5. However, by grouping the data for the last five years it can be seen in Table VII that out of the total puparia found on the main fly-round, the percentage found in Red Section is greatest at the period of peak adult concentration i.e., April and May. (*N.B.*—Data for the exceptionally severe 1st year had to be omitted because adult concentration took place abnormally early, and would therefore have masked the normal picture shown in Table VII.)

TABLE VII.—*Monthly variations in the degree of dry season pupal concentration recorded near the permanent pools of the Red Section.*

(Out of the monthly total of puparia found over 5 years on the main fly-round, the per centage occurring in the Red Section. R.P. = Red Section puparia. T.P. = total puparia.)

Months :—	XI.		XII.		I.		II.		II.		IV.		V.	
	R.P.	T.P.	R.P.	T.P.	R.P.	T.P.	R.P.	T.P.	R.P.	T.P.	R.P.	T.P.	R.P.	T.P.
Pupae :—	34	105	237	466	147	342	72	155	26	44	36	45	24	30
Percentage in Red	32		51		43		46		59		80		80	

On a basis of the length of the main fly-round sections, any figure over 56 per cent. may be considered as representing concentration within Red Section, see p. 95. The figures are regrettably small, and three mild years are included in the five dealt with; nevertheless these results strongly suggest that the puparia, as well as the adults, are to be found concentrated near the pools of permanent water in the months of April and May.

* * * * *

Repeated efforts were made to find the wet season breeding-grounds. Aerial sites such as rot holes in trees ranging from 3 to 15 ft. above ground-level were investigated; some such holes were filled with white sand to facilitate searching, but no puparia were found in them. The axils between palm fronds and the main trunk were searched without success, and equally fruitless were attempts to sieve the soil of the forest floor.

These negative results suggested the possibility that once the evaporation had fallen sufficiently in the early rains, *G. palpalis* larviposited in the adjacent open woodland, beyond the reach of the floods. Throughout the investigation

25 puparia and cases had been found *just* outside the forest fringe, some under logs—evidence which tended to support this contention.

It seemed possible that *G. palpalis* might be breeding in innumerable scattered sites throughout the woodland, and even in tussocks of grass as suggested for *G. morsitans* by Jackson (1937). It was decided whilst writing this paper to make one more attempt to elucidate the problem, by carrying out searches for pupal cases in such sites, but a month after the rains had ended when the soil would be dry enough to facilitate searching.

When we started these pupal searches the Katabu fly-rounds had already been closed for nine months; it therefore came as a surprise to find that flies were extremely scarce for the time of year. Since, however, there had been phenomenally heavy rains, totalling 66 in., it seemed likely that the decimation of the fly population was associated with this factor.

As suggested by the scarcity of adults, the pupal searching was not very productive. At Yellow Section 20 boy hours of searching produced only one full puparium; at Red and White Sections 14 boy hours of searching yielded only two full puparia, but at Green Section 32 boy hours of searching yielded 5 full puparia and 13 cases. (*N.B.*—Green Section would appear to have been less affected than the others.)

The cases and puparia in Green were all found either along the line of junction between the fringing forest and the savannah, or just outside in the wooded grassland; *none were found at any appreciable distance from the forest edge.* Eight cases were found under a log, 3½ in. in diameter, buried under grass and 8 yds. from the forest; 2 cases were found in transition woodland under a seedling *Borassus* palm, choked with grass; all the other puparia and cases came from traditional sites, either on the edge or just outside the fringing forest.

Some indirect evidence can be adduced which suggests that even in the wettest years *G. palpalis* does not larviposit throughout the woodland. Two fly-rounds were carried out in early December to confirm the impression that fly density had been enormously reduced; if these figures are compared with the average fly density for the first period of December for the previous seven years one gets the following results:

	Green.	Main fly-round.	Yellow.
Average number of flies caught in early December from 1944 to 1950	30	70	36
Number caught in early December, 1951 . .	33	15	10

Whereas the fly density of Green Section is slightly above average, that of the main fly-round and of Yellow Section is only about one-fifth to one-fourth of what it is normally.

There is no reason to suppose that exceptionally heavy rains would seriously affect the adult population, as *G. palpalis* occurs near the coast in places where the average rainfall may be as much as 356 in. But in a riverine habitat such as that of Katabu, exceptional flooding of the fringing forest might well destroy all the puparia, *providing breeding was confined to the immediate vicinity of the forest.* If that was the case one would expect the ill-effects to be less near the source than further down-stream where the catchment area is greater and tributaries swell the volume of water. In fact, both fly catches and puparia searches showed that Green Section, which is only half a mile from the source, was unaffected, whereas the lower sections were very seriously affected. *Had breeding taken place throughout the open woodland, the fly density of these lower sections would not have been affected by flooding.* From this indirect evidence we can make the following deductions :

a. *G. palpalis* does not breed far out in the open woodland in the heavy rains.

b. *G. palpalis* appears to breed in many scattered sites along the higher ground near the edge of the fringing forest, where the puparia are safe from inundation except in years of quite exceptionally heavy rainfall.

c. In such years the area near the source of a stream may prove to be a valuable survival focus, when inundation of the breeding grounds further down-stream has led to a great reduction in fly density.

(b) Results from Dissections of Females for Pregnancy.

Despite our failure to find puparia in any numbers in the wet seasons we were convinced that breeding must continue throughout that season to permit of the maximal fly densities recorded in August and September. Nevertheless, since Gordon and Davey (1930) had demonstrated by pregnancy dissections that there is a complete cessation of breeding in the heavy rains, near Freetown, where the annual rainfall averages some 150 in.—it became incumbent upon us to show that no such cessation occurred under our very different climatic conditions.

Since it was undesirable to remove and kill females from the Katabu fly-round stream, material was collected from different streams within a radius of 30 miles of Kaduna ; dissections were carried out for 21 months by junior staff, who were frequently checked by one of the writers.

Gordon and Davey used as their index of pregnancy the percentage of females with larvae *in utero*, but we feel that unless all the dissections are done by trained entomologists it is safer to use as an index the percentage of females with egg or larva *in utero* ; an egg can be mistaken for a first stage larva by the novice.

Under laboratory conditions Helen Mellanby (1937) very rarely found that ovulation had taken place with virgin female *G. palpalis* under 22 days old, and that with virgin females 4 or 5 weeks old only about one-third had an egg *in utero*. With wild flies we have never found a virgin female (as shown by empty spermathecae) which had ovulated, and doubt whether under natural conditions females ever remain virgin for long enough for ovulation to take place. Hence a wild female with an egg *in utero* can definitely be classed as pregnant.

The results are given in Table VIII. Out of 5545 females dissected, 75 per cent. had ovulated, having either an egg or larva *in utero*, and are classed as pregnant ; 4 per cent. were virgin, leaving 21 per cent. in the pre-ovulation stage which were neither virgin nor pregnant, i.e., having full spermathecae but empty uteri.

June to September inclusive are the months of the heaviest rainfall ; the average percentage pregnant for these months over the two years is 69 per cent., which is very little less than the figure of 75 per cent. for the whole 21 months ; hence there can be no question of a wet season cessation of breeding occurring in these latitudes. Whereas Gordon and Davey found 0 per cent. with *larva in utero* in the heavy rains, we found 36 per cent. in this condition. It is probable that a wet season cessation of breeding by *G. palpalis* is only found in areas of very great rainfall.

TABLE VIII.—*Monthly variations in the percentage of female* G. palpalis *which are pregnant or virgin.*

(From dissections of flies caught in the Kaduna area).

	First Season (1949–'50)			Second Season (1950–'51)		
Month.	Total ♀s dissected.	Per-centage pregnant.	Per-centage virgin.	Total ♀s dissected.	Per-centage pregnant.	Per-centage virgin.
July . . .	189	69	.	480	66	5
August . .	285	74	.	531	65	5
September . .	358	76	5	346	81	3
October . .	280	82	4	228	73	3
November . .	214	88	2	231	83	1
December . .	288	80	2	275	81	3
January . .	334	74	4	210	79	3
February . .	258	74	6	200	78	7
March . .	148	65	13	176	77	3
April . .	176	80	3	.	.	.
May . . .	54	72	4	.	.	.
June . .	287	62	8	.	.	.

Before studying Table VIII in detail it is necessary that the reader should realise that a high pregnancy rate does not necessarily denote a high breeding rate. For a proper understanding of this complex subject one must recall the tsetse embryology of *G. palpalis* as elucidated by Helen Mellanby (1937). This may be summarised as follows :

A. *Duration of stages at 24° C. for young females which have yet to produce their 1st larva.*

8 days uterus empty = 49% of total period.
3½ days egg in uterus = 21% ,, ,,
5 days larva in uterus = 30% ,, ,,

16½ days = total period.

B. *Duration of stages at 24° C. for older females producing subsequent larvae.*

1 day uterus empty = 11% of total period.
3½ days egg in uterus = 37% ,, ,,
5 days larva in uterus = 52% ,, ,,

9½ days = total period.

If the total population consisted of young flies one would expect only 51 per cent. to be pregnant, i.e., egg or larva *in utero* ; but if the total population consisted of old flies the pregnancy per cent. would be 89. Hence theoretically at this temperature the pregnancy rate could range between the extremes of 51 and 89 per cent.; the more young flies in the catch the lower would be the pregnancy rate, and the fewer the young flies the greater would be the pregnancy rate.

There can be no doubt that within limits the duration of the life-cycle of tsetse decreases as the temperature rises and increases as the temperature falls. Thus Jack (1939) showed that the interlarval period for old *G. morsitans* females ranged from 25 days at 18° C. (64° F.) to only 8 days at 30° C. (86° F.), and Helen Mellanby showed that with *G. palpalis* a reduction in temperature from 24–22° C. (75·2–71·6° F.) increased the pre-ovulation period from 7 to 11 days and the post-ovulation period from 8½ days to 17½ days. Similarly, numerous workers have shown that the duration of the pupal period of tsetse increases as the temperature falls, and decreases as the temperature rises.

We can thus postulate that a combination of low adult longevity with a rapid breeding rate due to high temperature would increase the proportion of young flies in the catch in the pre-ovulation stage and therefore reduce the percentage of pregnant females. Conversely, a combination of high adult longevity with a slow breeding rate would increase the proportion of old females in the post-ovulation stage, and so increase the pregnancy rate.

Hence under certain conditions a high pregnancy rate could indicate a low breeding rate, and a low pregnancy rate could indicate a high breeding rate; clearly pregnancy rates can be most misleading.

Returning to the first season in Table VIII, it will be seen that a peak pregnancy rate was reached in November in the cold weather, when the breeding rate, according to the laboratory workers, is slow, and when, as will be shown in the next section, adult longevity is rather high. This is one of those cases where a high pregnancy rate is believed to reflect a low breeding rate. The second year's figures are not so even, possibly because a different set of collecting grounds were being visited in addition to the old ones; nevertheless, there is a tendency towards high pregnancy rates in the cold months of the year.

It would be unwise to attempt any further explanation of these pregnancy figures, because they can be so misleading.

The percentage of virgin females is very low when we consider that the average figure of 4 per cent. for 21 months will include newly emerged females that have not had time to become fertilised. The high percentage of virgins in March of the first season of Table VIII, which was the very severe 6th year of the investigation, suggests a high proportion of young flies in the catch, the old individuals having been killed off by the severe weather; the low pregnancy figure for March may also reflect the presence in the catch of a large proportion of young females in the pre-ovulation period. A high percentage of virgins is not found in March of the second season, but may be reflected in the relatively high figure for February.

Unfortunately we have no reliable data upon the percentage of young (teneral) flies for the different seasons. Since the whole investigation was based on the marking and release of flies, it was necessary to ban the use of the normal test of trying to express the ptilinum, lest the flies be injured. Data based solely on feeling the fly to determine if the chitin was soft or hard gave very erratic results, doubtless due to the horniness or otherwise of the recorder's fingers, and the subjective element involved.

(c) Results from Observations Made during the Mass-Breeding of *G. palpalis* in the Laboratory.

A start was made on the mass-breeding of tsetse in November, 1950, the beginning of the cold season. Since the electric wiring of the new laboratories had not been completed, we were unable to raise the temperature, but increased the humidity by keeping the flies in wet sacking cupboards.

Flies were being bred in the fly-room from adults that had emerged from either laboratory-bred or field-collected puparia. The method of breeding described by Geigy (1948) was used, the flies being fed on guinea-pigs.

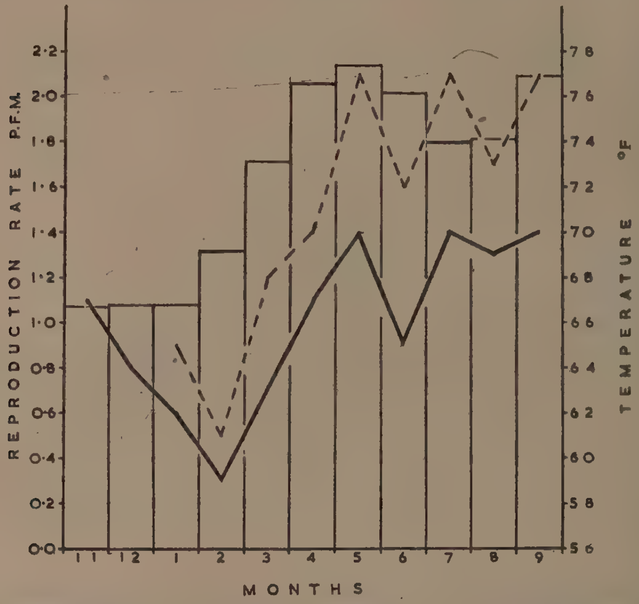

Fig. 8.—The reproduction rate in relation to temperature, under laboratory conditions.

[The reproduction rate, expressed as puparia per female per month, in the fly-room (line) and in the goat house (broken line); also the mean monthly temperature in the fly-room cupboard (columns).]

In addition, stocks of wild females caught in the field were kept for breeding purposes in an out-building which will be referred to as the "goat house"; these flies were kept in Bruce boxes and fed on goats.

The reproduction rate, expressed as the number of puparia per female per month (P.F.M.), was recorded monthly for each breeding establishment. These results are shown in fig. 8, together with the mean monthly temperature of the fly-room cupboard (columns), obtained from $\frac{\text{max.} + \text{min}}{2}$.

As is usual, the cold weather started suddenly at the beginning of November when the south-west monsoon gave way to the north-east harmattan wind; it continued until the end of January. It will be noted that throughout this period the breeding rate in the fly-room fell steadily, becoming minimal in February, a month after the end of the cold weather. The same fall in the breeding rate occurred in the goat house, which had nothing in common with the fly-room except the climate; the flies were of different origin, were kept differently, and were fed on a different host and kept in a different building by a different staff. There can be little doubt that this fall in the reproduction rate was associated with the cold weather; temperatures as low as 57° F. (13·9° C.) were recorded in the cupboard.[3] Metabolism must also have been greatly slowed down, because the pupal period in the fly-room extended to over 60 days.

Why the reproduction rate should be lowest in both fly-room and goat house a month *after* the cold weather had ended is hard to explain, because so little laboratory work has been done on this subject. Should the reproduction rate of the adult be influenced by the temperature at which the puparium had been kept, an acceptable explanation would be available. The population of flies in any month is composed of individuals of varying ages, so that the November flies would consist of flies which had mainly spent the pupal period in the much warmer conditions of October, whereas almost all the February flies would have spent the pupal period in the cold months of November, December and January.

We know from Helen Mellanby and others that with adults kept at abnormally low temperatures the reproduction rate is slowed down very greatly, but we do not know what is the effect upon the reproduction rate of adults which have spent their pupal life at very low temperatures, nor the effect upon the reproduction rate of keeping the female for the first part of her life at a low temperature and then transferring her to a high temperature for the rest of her life.

As the temperature rose in March, April and May, so did the reproduction rate increase. Subsequently, the mean temperature ranged between 74° and 77° F. (23·3–25° C.), and the reproduction rate fluctuated at a fairly high level.

Although hardly relevant to the subject of this paper, the reader may have observed that the reproduction rate among the wild flies kept in the goat house is always higher than that for the laboratory-bred flies kept in the fly-room. This is partly due to the fact that the percentage of unfertilised females is far higher among flies kept by the Geigy method than it is among wild flies.

The results described suggest that in the field there is probably a great decrease in the reproduction rate between November and February which would account for the great decrease in the fly population during these months; this decrease is then probably further augmented, despite an increase in the rate of breeding, by the ill-effects upon the adults of the great heat and dryness of March and sometimes of April. The result of this series of adverse climatic conditions culminates in the minimal fly density of April or May.

(d) The Temperature at which the Puparium Lives.

On p. 79 we mentioned how Burtt (1946*a*) had demonstrated with *G. morsitans* the importance of high pupal temperature in facilitating both the infection of the adult fly with *T. rhodesiense* and the subsequent transmission of this trypanosome. It is hoped that this work will be repeated with *G. palpalis* and

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[3] Humidity can be ignored, being permanently high in the sacking cupboards.

T. gambiense, because if similar results are obtained, it will strengthen our belief that the bulk of human trypanosomiasis in West Africa is transmitted at the season when both man and tsetse concentrate at the water holes—the *hottest* season of the year. With this object in mind we have collected data on the temperature of the pupal environment so that any laboratory work, of the type outlined above, can be planned to include the temperature range occurring in the field.

TABLE IX.—*The temperature conditions experienced in the field by the puparium of* G. palpalis.

(Data for 3 years; in brackets 6th year only.)

(a) *Temperature of soil at ½ in. depth.*

Month :— . .	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May.
Mean maximum temp. (° F.)	76·2 (73·4)	73·6 (72·5)	74·9 (76·0)	78·8 (81·8)	81·9 (86·6)	82·3 (81·7)	80·2 (81·3)
Mean minimum temp. (° F.)	59·9 (58·1)	58·2 (57·2)	59·9 (60·5)	61·8 (63·5)	65·6 (65·7)	69·9 (68·4)	71·4 (70·9)
Mean temp. (° F.) . .	68·1 (65·8)	65·9 (64·9)	67·4 (68·3)	70·3 (72·7)	73·8 (76·2)	76·1 (75·1)	75·8 (76·1)
Absolute maximum temp. (° F.)	88·1 (75·6)	78·1 (74·8)	81·5 (81·5)	86·0 (84·6)	89·6 (89·6)	88·7 (88·7)	84·6 (84·6)
Absolute minimum temp. (° F.)	52·3 (54·5)	54·5 (54·5)	56·7 (57·2)	55·8 (58·1)	51·7 (63·5)	64·8 (64·8)	68·0 (68·0)

(b) *Temperature of soil at 1½ in. depth.*

Month :— . .	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May.
Mean maximum temp. (° F.)	72·0 (71·1)	70·6 (70·7)	72·1 (73·8)	74·6 (76·8)	78·3 (82·6)	79·0 (79·3)	78·8 (79·9)
Mean minimum temp. (° F.)	61·5 (60·3)	59·2 (56·9)	60·4 (59·8)	62·0 (62·0)	65·6 (63·9)	69·7 (66·7)	71·1 (70·8)
Mean temp. (° F.) . .	66·8 (65·7)	64·9 (63·8)	66·3 (66·8)	68·3 (69·4)	72·0 (73·3)	74·4 (73·0)	75·0 (75·4)
Absolute maximum temp. (° F.)	77·9 (73·8)	73·8 (72·5)	77·9 (77·9)	79·7 (79·7)	84·3 (84·3)	82·5 (82·5)	83·3 (83·3)
Absolute minimum temp. (° F.)	56·8 (56·8)	54·5 (54·5)	57·2 (57·2)	56·3 (56·3)	61·6 (61·6)	63·1 (63·1)	67·3 (67·3)

For three years maximum and minimum soil temperatures have been recorded at ½ and 1½ in. depths. The thermometers have been moved at the beginning of each month to the site which has just been found to be most productive of puparia, so that the temperatures refer to current breeding sites and not to ones that may have been evacuated. Records have only been kept for the dry season and early rains when puparia are most readily found, but since these seasons cover the coldest and hottest months of the year, it is reasonable to suppose that the figures cover the temperature range experienced by the puparia throughout the year. In the heavy rains the mean soil temperature is probably a little over 70° F.

Table IX includes the average monthly maximum and minimum temperatures for the three years, from which a mean temperature has been calculated; in addition, the absolute maximum and minimum ever recorded during three years is shown for each month. The years dealt with are the 4th, 5th and 6th years of the investigation, and so include the mildest, the next mildest and the second most severe dry seasons of the six years of the investigation. Since we are particularly interested in abnormally severe dry seasons, figures for the 6th year are shown in brackets; when dealing with soil temperatures the differences from year to year are not very great, except for the maximum temperature in March.

Our general observations suggest that puparia are rarely found at a much greater depth than half an inch. Yorke and Blacklock (1915) did some critical work on this subject with *G. palpalis* at Freetown; out of 63 puparia, 51 were found in the first ½ in., only 10 between ½ in. and 3 in. depth, and 2 between 3 and 6 in. Hence our table for ½ in. depth is likely to be the most applicable.

There is every reason to consider that our three years of observations are representative; it can therefore be said that near the northern limit of the range of *G. palpalis*, which is both hotter and colder than further south, the temperatures of the pupal environment range approximately through the following limits: The extreme *absolute* temperatures range between 54·5° and 89·6° F. (12·5°–32° C.). The *mean* monthly minimum temperature may be as low as 57° F. (13·9° C.), and the *mean* maximum as high as 86·6° F. (30·3° C.). The *average* temperature of the pupal environment ranges from 65°–76° F.[4] (18·3–24·4° C.).

At 1½ in. depth the maximum temperature is never quite so high as at the ½-in level; the minimum temperature is about the same in the hot season, but not quite so low in the cold season. The mean temperature is never more than 2° F. lower at the greater depth.

(e) Conclusions.

1. In the early dry or cold season, despite a decreasing reproduction rate and a falling fly density, puparia are found in ever-increasing numbers until a peak is reached around December. This is partly because the soil becomes drier, making puparia much easier to find, and partly because the breeding grounds become concentrated into a much smaller area in or near the stream-bed.

2. By March, puparia become exceedingly scarce because the fly population has become so reduced.

3. In the early rains even fewer puparia are found because the fly population is minimal and wet soil greatly hinders the searchers.

4. During the heavy rains puparia are undoubtedly becoming far more plentiful, but cannot readily be found, presumably because of the wet soil and because the sites are far more scattered.

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[4] Nash (1948*b*) gives a figure of 79° for the hot season preceding this three-year period; however, we are now somewhat doubtful of the accuracy of the instrument used.

5. In the wet season *G. palpalis* appears to breed along the higher ground near the edge of the fringing forest, where the puparia are safe from inundation in years of normal rainfall.

6. Pregnancy dissections confirm that there is no wet season cessation of breeding near the northern limit of *G. palpalis*.

7. Reasons are given for supposing that, under certain conditions, a high pregnancy rate may really indicate a low reproduction rate, and a low pregnancy rate a high reproduction rate.

8. If these reasons are valid, the high pregnancy rate of the early, cold dry season indicates a reduced reproduction rate, a supposition that has been confirmed by the effect of the cold season upon the reproduction rate in the laboratory.

9. In the field the reproduction rate is believed to fall from November to February, and then to start increasing with rising temperature. But since very hot dry weather kills off many adults it does not effect an increase in the fly population until the rains are well established.

10. The temperature of the pupal environment has been recorded for three years. The average monthly temperature at ½ in. depth ranges from 65°–76° F. (18·3–24·4° C.); the mean monthly maximum temperature did not exceed 86·6° F. (30·3° C.), and the mean minimum did not fall below 57° F. (13·9° C.).

9. LONGEVITY AS RELATED TO SEASON.

The longevity of tsetse is of great importance epidemiologically, because, providing that other factors are favourable, the longer a fly lives the more likely it is to become infected—and the longer an infected fly survives after becoming infective the more damage it can do.

It has been found extremely difficult to obtain an indication of seasonal fluctuations in the longevity of *G. palpalis*. Four different lines of approach have been followed.

(a) Results from Marking and Liberating Laboratory-Hatched Flies.

Laboratory-hatched flies were marked, fed and liberated on the fly-round stream within 24 hours of hatching. The experiment was given up after 2 years when it was found that for these young flies the longevity figures, based on recaptures, instead of being greater, were considerably lower than those obtained by marking wild flies of an age unknown at the time of marking. Either flies that have emerged in the laboratory are constitutionally weaker than those that have hatched in the field, or possibly the marking of newly emerged tsetse, whose chitin has not properly hardened, may upset their flight. It certainly does not affect them chemically, because in the experiments described later it will be shown that *in captivity* young marked flies can live for many months.

(b) Results from Marking Wild Flies.

The data used throughout this section of the paper were obtained during the first four years of the investigation and are based on the recapture of 1155 females and 1619 males. Owing to the annual scarcity of flies in certain months of the year it has been necessary to group the monthly data for the 4 years; fortunately our seasons are very well-defined, and hardly ever vary in the date of their onset by more than a month from year to year. Longevity data are always shown against the month when the recaptured flies were marked, not against the month when they were recaptured; hence the data indicate the *expectation* of life of the fly population occurring in any month.

(i) Seasonal Variations in the Average Known Age of Recaptured Flies.

On each of the four days of the month when the fly-round was carried out, all unmarked flies were marked with the day's combination of colours on the pro- and mesothorax, and with the colour denoting "locality" on the scutellum; they were then liberated. Artist's oil paints were used.

From the marked flies subsequently recaptured we obtained the duration of *known* life. Flies recaptured within 24 hours of marking were ignored, because, having had insufficient time to disperse, they were taken in such large numbers that their inclusion would have greatly reduced the average known age.

After recording the markings, a recaptured fly was liberated without being re-marked; hence the same fly could have been recaptured and recorded several times. It was impossible to reserve sufficient space on the thorax for remarking if a simple, bold system was to be adopted which would provide sufficient combinations to cover periods of 7 months without repetition. With trustworthy junior staff of limited ability, it is wiser to sacrifice additional detail in favour of a simplicity that will lead to basic accuracy.

It should be noted that neither the date of birth nor death was known with these wild flies—only the *known* age between marking and recapture; however, it is reasonable to expect that seasonal fluctuations in the average length of known age will reflect seasonal variations in the average length of true age. It is fair to assume that the flies caught and marked on the fly-round *normally* represent a random sample of the population, and therefore that the average age of the sample on the day of marking corresponds to middle age; thus it should be permissible to double the figure for the average *known* age of the recaptures in order to obtain an approximation of the average true age. Even so, this figure—average known age × 2—*must* give an underestimate, because we still do not know the date of birth or death of each fly, only the known age. The method is admittedly crude, but it gives a remarkably consistent *indication* of seasonal variations in longevity.

In Table X the figures for known age × 2 indicate the average known expectation of life of that month's population.

Table X.—*Indicating the seasonal variations in the expectation of life among the wild flies caught in each month.*

(*Average known age, in days, of recaptured flies* × 2.)

	Dry season.					Wet season.						
Sex.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May.	June.	July.	Aug.	Sept.	Oct.
♀ .	64	46	40	48	54	106	84	76	68	66	64	74
♂ .	46	40	30	34	34	46	50	40	48	48	44	52

The females will be dealt with first because, since they live longer, it follows that there is a wider range in the seasonal variation of their expectation of life; this facilitates the elucidation of the cycle.

With the onset of the dry season and a rising saturation deficit, female expectation decreases rapidly. The females caught in January have the least expectation of life, which is understandable, because the extreme heat and desiccation of February and March prevent the achievement of old age by the January fly population; this will be confirmed later, when it will also be shown that these adverse conditions discriminate against the older individuals.

The female expectation of life progressively increases, albeit not very much, for the February and March populations, despite the increasing severity of the weather. This is because, having a shorter period of extreme conditions to face than the January flies, more individuals succeed in surviving until the start of the rains, after which the achievement of real old age becomes possible; the inclusion of such individuals increases the average known age for these months.

If the severity of the late dry season tends to act selectively against the older flies, we should expect that the April population would be composed of unusually young individuals, which, in view of the favourable weather ahead, should have an expectation of exceptionally long life. That this is so is very convincingly shown in Table X, where the expectation of female life is far greater for April than for any other month in the year.

The selective action upon old tsetse of a sudden change of weather in the late dry season is often observable among flies kept in captivity. Thus on 21st and 22nd February, 1948, the maximum temperature was 7° F. (4° C.) above the average for the previous 8 days, and the maximum saturation deficit, having increased by 4 mb., had almost doubled itself; further, the daily mortality amongst 261 tsetse kept in separate tubes in the stream-bed rose from under 1 per cent. to 7·5 per cent. The average age of this stock of flies on the day before the weather changed was 69 days, but the average age of the 36 flies that suddenly died was 82 days; of the dead flies, 14 were over 100 days old.

Returning to Table X, as a result of the selective action of March, the April population is unusually young, which is one reason for its exceptional expectation of life. As might be expected, with a return to a better balanced community in May the expectation of life falls; this fall continues throughout the wet season into September—the last and sometimes wettest month of the heavy rains. What is the nature of the adverse factor responsible is not known; however, it is associated with the months when the atmosphere in the stream-bed is nearly saturated, but when the temperature is steady at about the mean of the annual range. (As will be mentioned later, a very high mortality takes place amongst flies kept in tubes in the stream-bed during these months.) It will be noted that with the abatement of the rains in October the expectation shoots up without any lag, suggesting that the speedy removal of the adverse factor was associated with a return to a drier atmosphere.

Turning now to the seasonal fluctuations in male expectation given in Table X, it will be seen that they agree closely with those described for the female. However, the greatest expectation of male life is in May, not April, suggesting that this sex may be more susceptible to very hot, dry conditions, and therefore does not respond quite so quickly to the ameliorative effects of the early rains.

The apparent male divergence from the female trend between June and September is probably not significant as the range is very slight—40 to 48 days. Actually the average male figure for these 4 months is 45 days, as against 50 days for May and 52 days for October, suggesting that the males may also suffer from a reduced expectation of life in the heavy rains.

* * * * *

It should be noted that when the fly population has been reduced by the severity of the dry season to its lowest ebb in April, the expectation of life amongst the survivors is greatest, thus assuring the recovery of the decimated community. This subject will be discussed later under "Some factors affecting the seasonal fluctuations in fly density," where the data given in Table X are shown graphically in fig. 14, B.

(ii) The Seasons when Infected *G. palpalis* are likely to be of the Greatest Economic Importance, as suggested by Seasonal Variations in the Expectation of Life.

For practical purposes, flies that live less than 20 days can be ignored, as only under exceptional circumstances could they become infected, and even so they would be unlikely to claim more than one victim before dying. It seems more reasonable to take flies that will live over 30 days as being of definite economic importance.

In fig. 9 the percentage of the total recaptures known to have lived over 30 days has been plotted *against the month of marking*.

Dealing first with the females, there are two peak periods when over 50 per cent. are known to live longer than 30 days—a major peak in April, May and June, and a minor peak in October.

Of these two periods the first, which covers the first part of the rains, is considered to be particularly dangerous to man because in April and May one finds a maximal expectation of life, combined with a close man-fly contact at the water holes—a combination associated with the hottest temperatures of the year which may facilitate fly infection and transmission. One can visualise the April females, which have mostly emerged from puparia incubated in the heat of March, becoming readily infected in April and transmitting the disease in May, when the water holes are still frequented ; by June these flies will have started to recolonise the stream and may introduce the disease to adjacent villages. From the point of view of cattle trypanosomiasis, it is in April, May and June that the northward migration of the Fulani takes place ; great herds of cattle cross innumerable fly-infested streams on their way to the fly-free north where they will spend the heavy rains.

The minor peak period in October, when over 50 per cent. of the females are known to live longer than 30 days, will lead to there being many old flies in November ; but this is probably of little importance in the spread of human sleeping sickness, because the wells will be full, and even in the absence of wells there is no close, *personal* man-fly contact at the water holes, because the tsetse are still travelling widely. On the other hand, this period coincides with the start of the southward migration of the Fulani, so that the presence of many old tsetse may be of some veterinary importance.

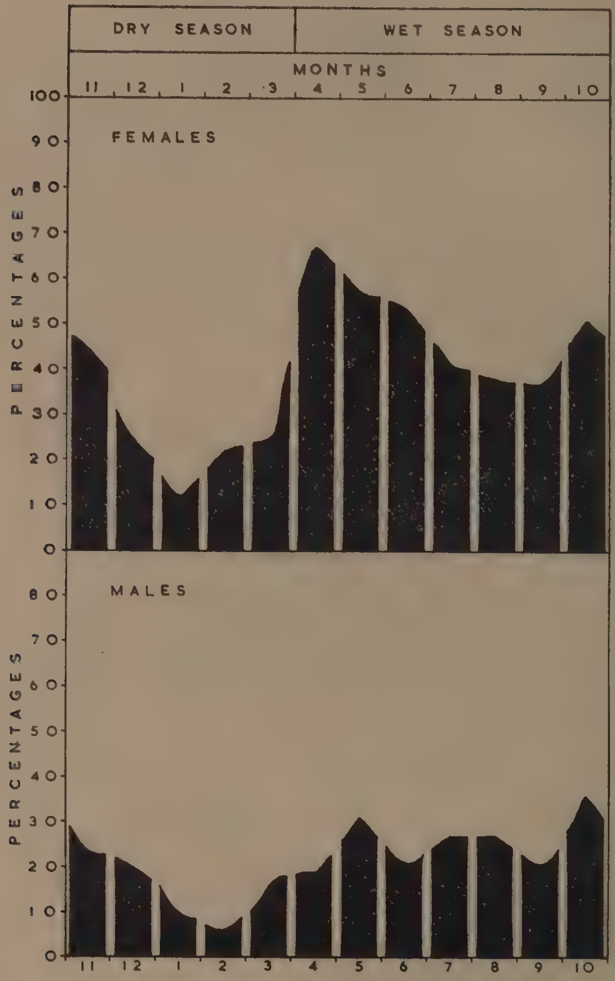


FIG. 9.—The time of year when infected *G. palpalis* are likely to be most dangerous, as suggested by their expectation of life.

(The percentage of the total recaptures known to have lived over 30 days, plotted against the month of marking.)

Although a much smaller proportion of males are known to live over 30 days, there is nevertheless a peak in May and October.

Turning now to the safest season, it is believed that the January flies are the least dangerous because they have a low expectation of life, and most of them will have spent their pupal or adult life under the coldest conditions of the year (Tables IX and II), which should mitigate against the flies becoming readily infected : as will be shown later, the infection rate amongst wild flies with trypanosomes of the *Vivax* group appears to be least in the cold season. In January only 12 per cent. of the females and 10 per cent. of the males are *known* to live over 30 days, as against comparable figures of 68 and 31 per cent. for April and May. (It must be again emphasised that these figures are known to be underestimates, because neither the date of birth nor death is available; but this should only affect the picture given in a matter of degree, not of principle.)

(iii) The Distribution of Recaptures in the Higher Known Age Groups.

Obviously it is important to have some idea of the proportion of the tsetse population that is likely to achieve *considerable* old age at the different seasons, even though it must be appreciated that, owing to the technique used, the proportions given are underestimates.

In Table XI the distribution of recaptures in the higher known age groups, is shown as a percentage of the total recaptures from each month's marking; 30-day age groups are used. The total recaptures on which the percentages are based include those from 0–30 days old, although this group has been omitted from the table as being irrelevant.

TABLE XI.—*The distribution of recaptures in the higher known age groups, expressed as percentages of the total recaptures.*

	Dry season.					Wet season.						
Month :—	XI.	XII.	I.	II.	III.	IV.	V.	VI.	VII.	VIII.	IX.	X.
Age groups.	Percentage in group.											
31–60 days :												
♀	36	21	8	13	9	15	31	31	25	23	21	30
♂	24	17	10	2	16	13	26	19	23	20	17	31
61–90 days :												
♀	8	2	2	8	14	36	12	20	9	8	11	19
♂	1	3	0	2	0	4	3	1	3	5	4	4
91–120 days :												
♀	0	1	0	1	2	15	14	1	5	6	2	2
♂	0	0	0	2	0	1	1	0	0	2	0	1

Whereas considerable numbers of both sexes achieve an age of 31–60 days, it is only females that attain an age of 61–90 days in appreciable numbers. In April, 36 per cent. of the female population is known to live from 61–90 days, and 15 per cent. are known to achieve 91–120 days; in this same favourable month, over 50 per cent. of the females have a known expectation of life of $2\frac{1}{4}$ to $4\frac{1}{4}$ months.

In Table XI flies living over 120 days have had to be ignored because their numbers are too small, as is shown by the following figures for the total number of flies recaptured in the highest age groups over 4 years:

	121–150 days.	151–180 days.
Out of 1155 females recaptured .	8 females	6 females
,, 1619 males ,, .	5 males	0 males

The number of females with over 120 days of known life form only 1·2 per cent. of the total recaptures; the similar figure for males is 0·3 per cent.

Clearly female *G. palpalis* live much longer than males, and should therefore be by far the most dangerous sex for spreading trypanosomiasis. A similar statement was made by Nash (1948*b*), and was subsequently challenged by Fairbairn and Culwick (1950, p. 39) on the grounds that the male of *G. morsitans* is a far more efficient transmitter of disease than the female, and that the male is the most active sex. But one cannot argue that what is found for one species of tsetse is bound to be correct for another. In the case of *G. palpalis* we have found no evidence that the male is always more active than the female; out of over 17,000 *G. palpalis* caught on our fly-rounds 49 per cent. were females. With regard to sexual differences in the infection rate in *G. palpalis*, we hold that there is *as yet* no evidence that the male is the more heavily infected sex. Burtt (1946*b*), discussing Duke's (1930) transmission experiments with *T. rhodesiense* and *T. gambiense* in relation to *G. palpalis*, based on 24,509 flies, describes how it was finally decided by Dr. C. H. N. Jackson's statistical analysis of Duke's figures that there was no significant difference between the salivary gland infection rates of the two sexes. Unfortunately there is little evidence of general infection rates among wild *G. palpalis*; however, out of 3226 proboscis dissections of *G. palpalis* carried out by Squire (1951) in Sierra Leone the infection rate was 5·8 per cent. for females and only 3·7 per cent. for males; but out of only 344 wild *G. palpalis* dissected by Fontoura de Sequeira (1935) in Portuguese Guinea the infection rate was 6·9 per cent. for males and 5·2 per cent. for females.

It may be concluded that, providing the two sexes do not differ markedly in their ability to become infected, the female of *G. palpalis* must be the more dangerous sex because of her greater length of life.

(c) Results from Marked Flies Kept in Tubes in the Stream-bed.

Knowing that our results on longevity obtained from the recapture of marked wild flies *must* be giving a conservative index of age, it was decided to keep newly hatched *G. palpalis* in individual tubes in the stream-bed, and from these to ascertain the potential longevity of the species.

Within 24 hours of hatching, adults were marked, fed, tubed, taken down to the fly-round stream and placed in two well-ventilated boxes—one box was kept at 4 ft. above ground-level and one at 4 in. In the dry season the boxes were suspended over a pool in the Red Section, but in the rains when the stream floods they were kept on the bank, but still under heavy, low shade. Daily, each fly was given an opportunity to feed off a goat. The flies were marked so that the results would be more comparable with those obtained from the marked wild flies.

Owing to the early segregation of the tsetse into individual tubes the females were mostly virgin; however, an experiment, in which the longevity of fertilised and unfertilised females was compared, showed no significant difference in the ages achieved by each group.

(i) A Comparison between the Longevity of Wild and Tubed Flies in the Dry and Wet Seasons.

Since the tubed flies had an assured food supply and were thus spared all the hazards associated with the search for food under natural conditions, they should theoretically live longer than wild flies. Since we already had figures for the expectation of life of wild flies (Table X), which were known to be underestimates, it was obvious that our figures for tubed flies would be greater, *unless* there was something wrong with their environment.

It will be seen from Table XII that throughout the dry season the longevity of the tubed flies was considerably greater than the figure for the wild flies, but that throughout the rains there was a cataclysmic fall in the longevity of the tubed flies, indicating that the environment had become exceedingly unfavourable.

TABLE XII.—*A comparison between the longevity of wild and tubed flies in the dry and wet seasons.*

	Wild flies. (Average known age × 2.)		Tubed flies. (Average age.)		Tubed fly average differs by :—
	Number of flies.	Days.	Number of flies.	Days.	Days ±.
Dry season . .	506 ♀	54	566 ♀	88	+34
	505 ♂	39	379 ♂	53	+14
Wet season . .	649 ♀	78	247 ♀	51	−27
	1,114 ♂	46	281 ♂	30	−16

The tubed fly data for the dry season are considered to be valuable, but that for the rains to be worthless. In the rains the tubed fly is compelled to live in a very high humidity and is denied the exercise of flight and the warmth of the sun. But under the desiccating, dry season conditions the tubed fly is living close to water and in the shade—as does the wild fly at this season except when forced to look for food.

The adverse factor, associated with very high humidity, which in the heavy rains causes a decrease in longevity and finally in fly density, may well be intensified for the tubed flies ; but the adverse, dry season factors—desiccation and high temperature—may well be mitigated for these flies, which never have to leave the water's edge in search of food.

It is most unfortunate that owing to the failure of the tubed fly experiment in the rains it was impossible to obtain figures for the potential longevity of the species at this season.

(ii) A Comparison of Longevity at Four Feet and Four Inches above Ground-level.

The females kept at 4 ft. lived longer than those kept at 4 in. for 15 out of 19 months, but the males lived longer at 4 ft. for only 9 out of 19 months, and it was clear that this sex did better in the hot season near ground-level, but better in the rains at 4 ft. The results suggest that the females are more resistant than the males to hot, dry conditions, and that in the rains both sexes do best if kept in the less humid conditions at 4 ft. This subject will shortly be gone into in greater detail in connection with another experiment. (*N.B.*—The data used in Table XII and fig. 10 refer to the figures for both heights combined ; this was necessary in order to obtain adequate numbers, but may have resulted in having somewhat depressed the male age in the latter part of the dry season.)

(iii) The Dry Season Distribution of Mortality in Age Groups for both Male and Female *G. palpalis.*

In fig. 10 the distribution of deaths among tubed flies kept in the stream-bed is shown by 20 day age groups; it is based on 571 females and 380 males, which were kept from October to March inclusive in two consecutive years.

It was found from the wild fly marking experiment that the October flies had a very considerable expectation of life, but that the January flies had a minimal expectation; hence the six-month period selected for the tubed flies covers a wide range of favourable and unfavourable conditions in the field, conditions which although probably mitigated in the tube experiment, are nevertheless reflected by the following figures, which also serve to confirm the marked, wild fly results:

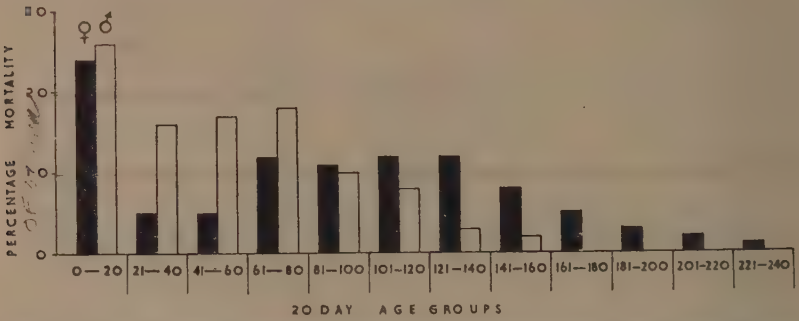


FIG. 10.—The dry season distribution of mortality in age groups, for both male and female *G. palpalis.*

(Expressed as the percentage mortality falling into each 20 day age group.)

> Out of 89 females born in October, 63 per cent. lived over 80 days, whereas in January, out of 81 females, only 38 per cent. lived over 80 days. Similarly with the males—whereas 33 per cent. of 64 males born in October lived over 80 days, only 8 per cent. of 72 males born in January succeeded in doing so.

A study of fig. 10 reveals some interesting facts. The span of female life is longer than that of males. About 25 per cent. of both the male and female populations die within twenty days of birth and therefore are most unlikely to become transmitters of trypanosomiasis. Out of the 75 per cent. survivors, about half the female population can expect to live between 60 and 140 days, whereas a similar proportion of the males has an expectation of only 20 to 80 days of life. Whereas 11 per cent. of the females may live from 160 to 240 days, virtually no males can achieve this degree of longevity.

The curve for the females (solid) should be noted. After a high "infantile mortality" during the first 20 days, the curve drops and there is a period of

40 days with an extremely low mortality; the curve then rises and remains steady for 80 days, during which time nearly half the total deaths occur, i.e., between the 61st and 140th day; the curve then falls steadily as the remaining fifth of the population dies between the 141st and 240th day. The curve for the males tends to follow the same course, but is telescoped into a much shorter period, three-quarters of the population being dead by the 80th day, as against the 130th day for females.

(d) Extremes of Old Age Attainable by *G. palpalis*.

Females: At Katabu a marked female fly has been recaptured with 184 days of known life. In East Africa, Carpenter (1912, 1913) recaptured a marked female with a known life of 182 days.

The greatest age achieved by a tubed female fly in our experiments was 233 days. In East Africa, Kleine and Fischer (1911) managed to keep a female alive for 227 days.

It may be concluded that wild females can definitely achieve a life-span of 6 *calender months, and that in captivity they may achieve almost* 8 *months.*

Males: At Katabu a marked male fly has been recaptured with 143 days of known life. Carpenter (1912, 1913) recaptured a marked male at the end of the rains with a known life of 149 days. (In the early rains Carpenter claims to have recaptured two males with a known life of 247–253 days; but since the oldest female for this same season was only 126–131 days old, it is suggested that this record should be viewed with the gravest suspicion. Since his marking technique consisted of the amputation of the tibia or femur of different legs, it is possible that these two males had received accidental injury, which simulated marking.)

The greatest age achieved by a tubed male in our experiments was 168 days. In East Africa, Fraser and Duke (1912) found in laboratory experiments that the male could live up to 150 days.

It may be concluded that wild males can definitely achieve a life-span of almost 5 *calendar months, and that in captivity they may achieve* 5½ *months.*

(e) A Comparison of Late Dry Season Mortality among Flies Kept in Tubes in the White and Red Sections.

The experiments described under this section were carried out by Mrs. M. Page. We are deeply indebted to her for having generously decided not to publish her results as a separate paper, but to allow us to incorporate them in this monograph, where they provide an important facet in the overall picture.

On pp. 95–98 it was shown that in years in which the climatic conditions were severe in the late dry season, *G. palpalis* virtually evacuated the White Section in favour of the permanent pools of Red Section. It was therefore desirable to ascertain what exactly would happen to flies if they were kept in tubes in the White Section, during the months when the wild flies had evacuated the area.

The work was undertaken during the 6th year of the investigation, which was the second most severe year experienced.

During the first ten days of January newly-hatched *G. palpalis* were marked, put into separate tubes, and fed within 24 hours of emergence. After a further

24 hours, any tubes with dead flies were discarded and the remaining tubes divided into four equal groups with the same proportion of males to females in each: they were then taken down to the fly-round stream-bed and were placed in four well-ventilated boxes, two in White Section, one at 4 ft. and one at 4 in. above ground-level, whilst the other two boxes were placed in Red Section at similar heights but suspended above a pool of water. By 10th January the stock in each box had been made up to 100 flies.

Every day, all flies were given a chance to feed on a goat and all deaths were recorded.

At the beginning of February and March, 28 and 23 tubed flies respectively were added to each box; these numbers for the replenishment of stock were based on the number of deaths recorded from the box which showed the *least* mortality during the previous month. The idea was to replace *normal* wastage due to normal death with young flies and so obtain a population of varying ages, upon which any discriminatory effect of the very severe conditions of March and April could be observed. (Actually the lowest mortality for January was only 9 flies, but 28 were added to all boxes in early February, to compensate for 19 flies killed by ants at Red Section, 4 inches.) To summarise, each box received during the three months 100 + 28 + 23 flies = 151 flies.

When the first rain fell on 20th April the experiment was closed, even though some flies were still alive. Had the experiment been continued, the subsequent deaths might not have been associated with the adverse dry season factors, but with the adverse wet season factor—which would have confused the issue.

Dry and wet bulb readings were obtained from recording thermohygrographs, kept in four Stevenson screens, one adjacent to each box.

(i) The Effect upon Flies of being Kept in the White Section throughout the Late Dry Season.

Table XIII shows that none of the flies kept at 4 ft. in the White Section lived until the end of the experiment on 20th April—not even those born in early March. At 4 in. only 1 per cent. of 151 flies survived, and these were all

Table XIII.—*The late dry season survival among tubed flies, in relation to situation.*

(Out of the total flies comprising each month's batch, the percentage which survived until 20th April.)

Situation.	Percentage survival. January batch.	February batch.	March batch.	All batches combined.
White, 4 ft.	0	0	0	0
White, 4 in.	0	0	9	1
Red, 4 ft.	3	7	35	9
Red, 4 in.	14	29	52	24

(*N.B.*—Except in January, the figures upon which these percentages are based are very small, so that attention should be concentrated on the very obvious trend, rather than on the actual size of the percentages. Owing to the labour required to feed individual flies it was impossible to use larger numbers; as it was, some 400 flies had to be fed daily in January and February.)

from the March batch. Clearly, unless the wild fly population of the White Section sought sanctuary in Red, it would almost certainly be exterminated. It should be remembered that wild flies would not have the advantage of an assured food supply, but would frequently have had to expend energy and fly at a greater height in order to find their hosts.

(ii) A Comparison of Mortality in Relation to the Climate of the White and Red Sections.

The conditions under which the flies of the four boxes were kept were identical except for climate. Attempts to correlate daily mortality with daily fluctuations in the maximum temperature and maximum saturation deficit failed, presumably because climatic conditions were never such as to prove *immediately* lethal. Consequently the results were grouped by ten-day periods. The mortality during each period was expressed as a percentage of the stock alive at the beginning of that period. The average maximum temperature and maximum saturation deficit were worked out for each ten days.

For convenience, the three months of the experiment are regarded as each being of 30 days' duration, i.e., January 0–30 days, February 31–60 days and March 61–90 days.

In fig. 11 the data for the two extreme situations only are compared—White, 4 ft., and Red, 4 in.; the results for the other two situations provide pictures in between these two extremes. The mortalities for the three separate monthly batches are shown individually by three different curves, so that the effect of the climate of any particular period upon young, middle-aged and old flies can be studied. The average maximum temperature is shown by columns which embrace the full width of each ten-day period; the mean maximum saturation deficit is shown by narrower shaded columns within the temperature columns. The three periods in each month are numbered 1st, 2nd and 3rd for ease of reference. Along the bottom, the days are shown in three lines so that the approximate age of each month's flies for any particular 10-day period can be quickly ascertained; but it should be remembered that each month's batch of flies hatched during the first 10 days of the month, so that the ages shown tend to be a few days too great.

Dealing first with the flies kept at 4 ft. in the waterless White Section, no very serious mortalities occurred until the sudden rise in temperature and saturation deficit in the last period of February.

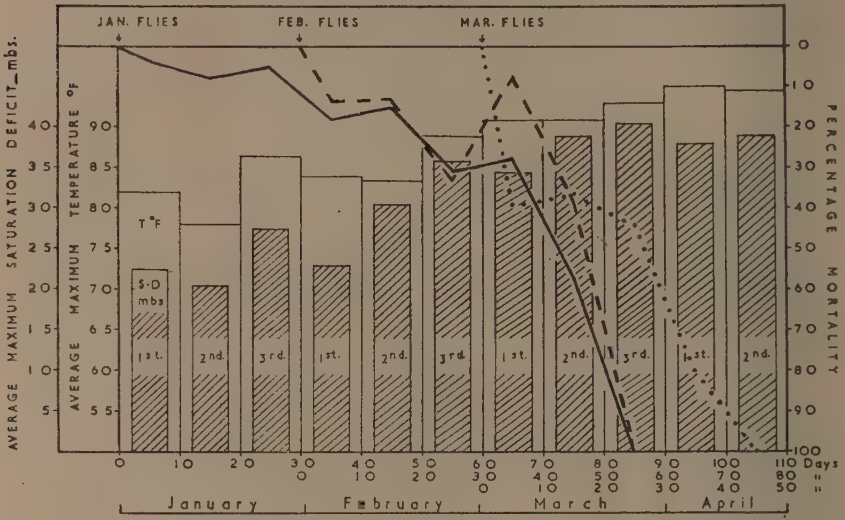
A study of the mortality percentages between the end of February and early April suggests the following conclusions:

a. Flies 0–10 days old are more susceptible to severe conditions than older flies, see 1st Period March and compare mortality of March batch with that for January and February batches.

b. Flies from 10–50 days old are less susceptible than flies from 50–90 days old, see:—

1st Period March, cf. February with January batch.
2nd ,, ,, cf. February and March with January batch.
3rd ,, ,, cf. March with January and February batches.

THE MORTALITY & CLIMATE AT 4 FEET IN A WATERLESS STRETCH OF STREAM (WHITE SECTION)



THE MORTALITY & CLIMATE AT 4 INS. ABOVE WATER, IN A STRETCH OF STREAM WITH POOLS (RED SECTION)

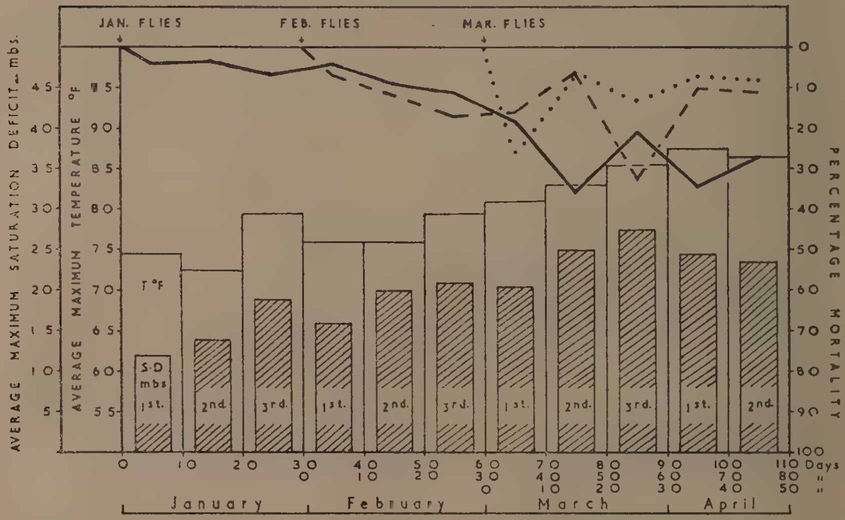


Fig. 11.—A comparison of late dry season mortality in Red and White Sections.

(Mortality for each 10-day period expressed as a percentage of the stock alive at the beginning of the period.)

It is most striking how, in the 3rd Period of March, conditions which exterminated the January and February flies failed to kill all the younger March flies. It should be noted that the degree of mortality for the March flies between 0–30 days old was far greater than for the January and even the February flies which spent this age under much milder conditions.

(*N.B.*—The impression given by the upper half of fig. 11 that the January wild flies should have a greater expectation of life than the March flies is, of course, simply due to the fact that the tubed flies were compelled to live in the waterless White Section until exterminated by the rigours of March. Wild flies would have evacuated this section in favour of Red, where, as already shown in Table X, the March flies would have had the greater expectation of life.)

Turning now to the lower half of fig. 11, at Red Section, 4 in., both the climate and the mortality curves are entirely different from those just described for the waterless White Section. The January and February flies did very well; no heavy mortality occurred amongst the January batch until March, 2nd Period, when they were 70–80 days old; the February flies suffered no high mortality until they were 50–60 days old. However, the March flies did suffer a much greater infantile mortality than was experienced by those of the two previous months, cf. 1st Period March, with 1st Periods for January and February. This fact, combined with the fact that the February flies experienced their first heavy mortality at a rather younger age than did the January flies, suggests that possibly by March conditions were becoming rather unfavourable, even in the vicinity of water.

In view of the above results, it is not surprising that in March of this 6th year, 87 per cent. of the wild flies caught on the main fly-round were found in the Red Section.

(iii) The Relationship between High Mortality and Climate.

It had been anticipated that definite data would be obtained indicating that, in any of the four situations investigated, an abnormally heavy mortality would always occur after either the maximum temperature or the maximum saturation deficit had reached a certain critical point. It was hoped to discover these points, which were expected to prove to be the same for all sites. However, it has been found that in the case of saturation deficit, the critical point differs—the drier the site, the higher the critical point. This suggests that flies, acclimatised in early life to arid conditions, will be able to tolerate a greater degree of aridity than flies which have started life under more humid conditions.

The relationship between the degree of mortality and the corresponding degree of average maximum saturation deficit and temperature for the same period are shown for all four sites in figs. 12 and 13, where the mortality has been plotted against the climatic factor. Since there is an obvious relationship—mortality increasing with an increase in the climatic factor—curves have been drawn as suggested by the distribution of the points. The mortality percentages for each 10-day period are based on the deaths and stock of both the January and February batches combined; the March flies were omitted because being so much younger, their high infantile mortality and subsequent greater resistance would, by their inclusion, have obscured the picture in

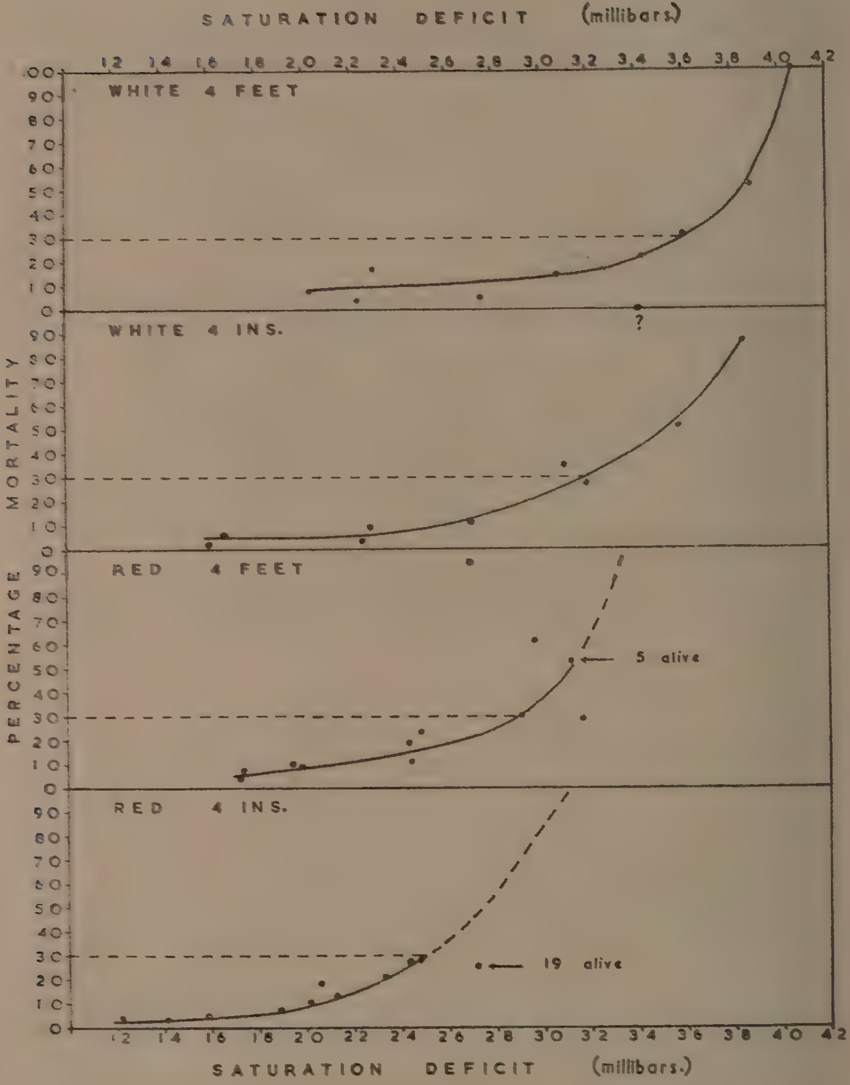


Fig. 12.—The mortality per cent. in relation to maximum saturation deficit.

(Using both the January and February flies, the mortality per cent. for each 10 day period, plotted against the average maximum saturation deficit for that period.)

March when the high mortalities occur in all flies except those in early middle age; this can be seen from the top half of fig. 11. A mortality of 30 per cent. in a 10-day period is undoubtedly abnormally high; as a guide to the eye, a dotted line has been drawn along the 30 per cent. line in figs. 12 and 13 until it meets the curve.

* * * * *

In fig. 12 mortality has been plotted against the average maximum saturation deficit. Clearly, within certain limits, *mortality increases with increasing saturation deficit.*

If the saturation deficit reading, at the intersection of the 30 per cent. mortality line with the curve, is recorded for each site we get the following readings:

White, 4 *ft.* 30 per cent. mortality occurs at about 36 mb.
White, 4 *in.* ,, ,, ,, ,, ,, 32 mb.
Red, 4 *ft.* ,, ,, ,, ,, ,, 29 mb.
Red, 4 *in.* ,, ,, ,, ,, ,, 25 mb.

At the first site, where the saturation deficit ranged from about 20 to 40 millibars (15–30 mm.), a 30 per cent. mortality was associated with 36 mb. (27 mm.); but at the fourth, mildest site where the range was only from 12 to 27 mb. (9–20 mm.), such a mortality was associated with only 25 mb. (19 mm.). It would therefore appear that *flies which are conditioned in early life to drier conditions can tolerate higher maximum saturation deficits than those accustomed to more humid conditions.*

The upward termination of the curves suggest that the upper fatal limit which leads to 100 per cent. mortality may be about 40 mb. (30 mm.) for the conditioned flies but only 31 mb. (23 mm.) for those from the mildest site. There would have been no point in keeping the surviving Red Section flies until they all died, as from the break of the rains on 20th April the saturation deficit crashed down; hence their eventual death would not have been associated with high saturation deficit, but due to normal causes. (*N.B.*—The point, on the 100 per cent. mortality line, marked with an interrogation mark under White, 4 in., was ignored when drawing the curve, because it was based on the last 3 flies; these, having just survived the peak saturation deficit of 38 mb. died in the following period when the saturation deficit was lower.)

* * * * *

In fig. 13 mortality has been plotted against the average maximum temperature. Clearly, within limits, *mortality increases with increasing maximum temperature.*

Studying the intersection of the 30 per cent. mortality lines with the curves, we find the following:

White, 4 *ft.* 30 per cent. mortality occurs at about 89° F.
White, 4 *in.* ,, ,, ,, ,, ,, 88° F.
Red, 4 *ft.* ,, ,, ,, ,, ,, 88° F.
Red, 4 *in.* ,, ,, ,, ,, ,, 88° F. ?

There is no evidence that any appreciable conditioning takes place, such as would enable flies from the hotter sites to withstand greater maximum temperatures than those from the cooler sites. *Average maximum temperatures of about* 88° *F.* (31° *C.*) *are associated with abnormally high mortality.* Geigy (1948) describes how, when trying to rear *G. palpalis* in a room with makeshift methods of climatic control, he found that when in summer the temperature reached 86° F. or over, many deaths occurred amongst his flies.

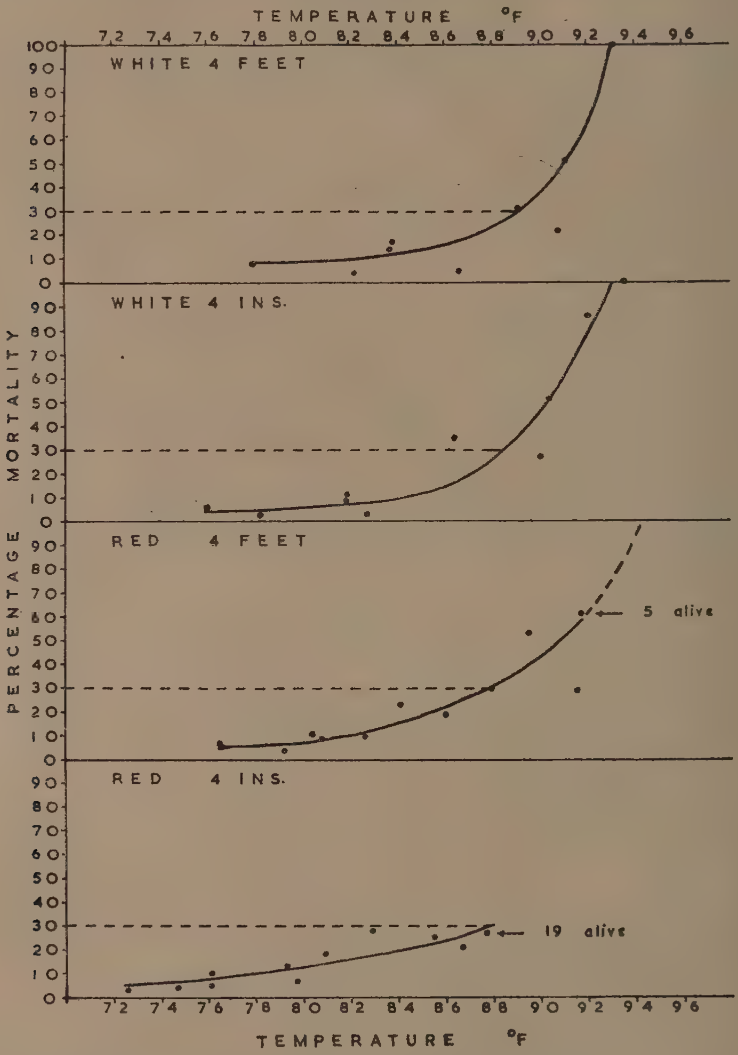


Fig. 13.—The mortality per cent. in relation to maximum temperature.

(Using both the January and February flies, the mortality per cent. for each 10 day period, plotted against the average maximum temperature for that period.)

If the upward termination of the curves is studied for the first three sites, it would appear that the *upper fatal limit for* G. palpalis *is associated with maximum temperatures averaging* 93–94° *F.* (34–34·5° *C.*). This is very different from Mellanby's results (1936), which show that 3 hours' exposure at 104° F. (40° C.) is the upper fatal limit; but such laboratory results are most misleading to the field worker. Under natural conditions the attainment of a maximum temperature of, say, 94° F. means that the flies have been subjected for some hours to temperatures over 90° F., both before and after the maximum is reached; further, our figures are based on the repetition of such a state of affairs for ten days. It should be mentioned that in the data used for fig. 13 the *absolute* maximum temperature never rose above 96° F. (35·6° C.).

No attempt has been made to plot mortality against the *mean* temperature, because the relatively low minimum temperatures of March depress the mean, and so tend to mask the fact that this is a month of dangerously high maximum temperatures.

* * * * *

(iv) Sexual Differences in Mortality in Relation to Climate.

The basic data used hitherto have been further analysed so that the monthly mortality of the two sexes, under identical climatic conditions, can be compared. By using the data for each of the four sites over the three months of the experiment, a wide range of climatic conditions has been obtained.

If Table XIV is read from the top, downwards, for each month, it will be seen that the four sites are arranged in order of increasing climatic severity; there is only one exception—the temperature for January, White Section, at 4 in. The reading of the table from left to right shows the increasing severity of the climate of each site as the dry season advances.

TABLE XIV.—*Sexual differences in the Monthly mortality per cent., in relation to the severity of the climate.*

	January.				February.				March.			
	Mortality per cent.		Mean maximum.		Mortality per cent.		Mean maximum.		Mortality per cent.		Mean maximum.	
	♂. %	♀. %	S.D.	T.°.	♂. %	♀. %	S.D.	T.°.	♂. %	♀. %	S.D.	T.°.
Red (pools), 4 in. .	13	12	15 mb.	76° F.	31	12	19 mb.	77° F.	65	38	24 mb.	83° F.
Red (pools), 4 ft. .	27	12	18 mb.	80° F.	54	19	24 mb.	82° F.	82	57	28 mb.	88° F.
White (dry), 4 in. .	12	10	18 mb.	79° F.	55	33	27 mb.	83° F.	92	88	35 mb.	91° F.
White (dry), 4 ft. .	22	12	23 mb.	82° F.	70	28	31 mb.	85° F.	92	92	38 mb.	92° F.

Reading the table downwards, month by month, shows that in January at the lesser heights the mortality rate amongst the two sexes was almost identical, but that at 4 ft. it was rather higher amongst males. However, under the severer climatic conditions of February and March, the mortality amongst males, irrespective of height, was consistently much greater, except under the extreme conditions experienced in the White Section for March, when the very high mortality rates became almost identical for the two sexes. If the table is read across from left to right, the same picture will be obtained.

It would seem from the above that under relatively mild conditions there is no very marked disparity in the mortality percentages of the two sexes, but under more severe conditions the males, having a lower threshold, are seriously affected by conditions which have relatively little effect upon the females. When, however, conditions become extreme with maximum temperatures approaching 93–94° F.—conditions which were shown by fig. 13 to represent the upper fatal limit—then the critical point for any surviving males is the same as for females.

Table XIV is based on periods of 30 days and not 10 as was the case in figs. 12 and 13, and is therefore far less accurate. It should not be used either to elucidate the climatic conditions associated with the threshold of abnormal mortality, or for comparison with the results from figs. 12 and 13; its purpose is to demonstrate, in publishable form, that the male definitely *has* a lower threshold than the female.

A table has been drawn up exactly like Table XIV except that it has been subdivided into 10-day periods; however, being 2 ft. in length it is hardly suitable for publication. If we again consider that a 30 per cent. mortality amongst stock in only 10 days is abnormally severe, this table indicates that with males the threshold for such a death-rate is associated with a mean maximum temperature of only 84° F. (28·9°C.), but for females the comparable figure is 91° F. (32·8° C.), cf. 88–89° F. for *both* sexes combined, as suggested by fig. 13. The critical mean maximum temperature for both sexes at which a mortality of 80–100 per cent. occurs ranges from 93°–95° F. (34–35° C.), cf. 93°–94° F. as suggested by fig. 13.

As has already been shown, one cannot expect to obtain a definite threshold and critical point for mortality associated with any particular saturation deficit. Nevertheless, the relationship between mortality and saturation deficit is similar to that between mortality and temperature, in that the trend is similar. This can be seen by reading Table XIV across and comparing sexual differences in mortality, month by month, for the *same* site; whereas male and female mortalities tend to be similar at low and very high saturation deficits, mortality is much higher among males at intermediate saturation deficits.

It may be concluded that the females are more tolerant to high temperature and saturation deficit than the males.

If this is so, and the severe conditions discriminate against the males, one would expect that by the end of the late dry season the wild fly population would have a preponderance of females. This is hard to prove. Certainly, the females per cent. figures for the fly-round tend to be greatest in January, February and March, p. 102 and fig. 6, but other factors are probably involved.

A confirmatory indication that there may well be an excess of females at this season is provided by a comparison of the expectation of life figures for marked wild males and females given in Table X; if the ratio of the female expectation of life to that of the males is worked out the figures are

December.	January.	February.	March.	April.	May.
1·2	1·3	1·4	1·6	2·3	1·7

In December, the coldest month, there is little difference between the expectation of life of the two sexes, but as the temperature rises throughout the late dry season and start of the rains, the ratio increases until in April the female expectation is more than twice as long as that of males ; this tremendous change in the ratio suggests that the male life may have been greatly curtailed by an increased mortality which discriminated against this sex.

From Table XIV it may also be concluded that in the same locality males survive the late dry season better at 4 in. above ground-level than at 4 ft., whereas females survive equally well at either height until the extremes of March, when they also do better at 4 in.—except in White Section, where the climate at both heights is almost identical and is near the upper fatal limit.

(f) Conclusions.

1. At the extreme end of the rains the expectation of life of both sexes is temporarily high. It then falls rapidly to become minimal in the mid-dry season, because the attainment of old age will be rendered impossible by the approaching rigours of the late dry season which discriminate against the older flies. At the start of the rains the expectation of life is greatest because the surviving population is young and has some months of very favourable conditions ahead. As the rains become heavier, expectation decreases slightly but steadily ; this trend is abruptly reversed as soon as the rains start to abate.

2. *a.* Flies infected during the first three months of the rains and at the close of the wet season are potentially the most dangerous, because of their high expectation of life.

b. Flies infected at both these times are likely to be dangerous to the Fulani cattle, which make their northern and southern migrations in the early rains and early dry seasons respectively.

c. The flies found at the start of the rains should be singularly dangerous as vectors of human trypanosomiasis. They will have hatched from pupae that were subjected to the highest temperatures of the year, and will continue to live under conditions of high temperature, which may cause them to become readily infected. Close personal man-fly contact persists at the water holes during the first two months of the wet season. Later, as the rains increase and these same flies disperse to re-colonise the stream they are liable to introduce the disease to adjacent villages.

d. The fly community at the close of the rains, despite its high expectation of life, is unlikely to be of much medical importance, because there will be no personal man-fly contact at the water holes, and many villages will be using their replenished wells.

3. Owing to the very low expectation of life of the mid-dry season fly population, these flies should be the least dangerous, especially since they will have emerged from puparia kept at very low temperatures, which may have reduced their infectibility.

4. The average age of the tsetse varies according to the season. A conservative estimate of the *average* age of wild females ranges from 6–15 weeks, and for wild males from 4 to nearly 8 weeks.

5. *a.* Whereas the percentage of females recaptured with an age known to exceed 2 calendar months is frequently high and may exceed 50 per cent., with males the percentage is low and never exceeded 7 per cent.

b. During four years the total number of females with over 4 calendar months of known life formed 1·2 per cent. of the total recaptures; for males the figure was 0·3 per cent.

* * * * *

6. *a.* To obtain an insight into the potential longevity of *G. palpalis*, flies were kept in tubes under supposedly ideal conditions in the stream-bed. In fact, the results for the rains were valueless as longevity was unnaturally low; confinement would appear to have intensified the factor associated with an almost saturated atmosphere, which led to a reduced longevity among the wild flies. But in the dry season longevity was excellent and the following results were obtained:

b. About one-quarter of the flies of each sex die within twenty days of birth.

c. The results for the females show that after the high, initial "infantile" mortality, there follows a period—21 to 60 days—in which very few deaths occur; about half the females die between the 61st and 140th day; the remaining one-fifth die between the 141st and 233rd day.

d. The results for the males show that after a high "infantile" mortality there follows a period of lower mortality, but nevertheless by the 80th day three-quarters of the males are dead. The remaining quarter die between the 81st and 168th day.

7. From our experiments, and those of other workers, on the *extremes* of age attainable by *G. palpalis*, it is concluded that at favourable seasons females in nature can definitely live up to 6 calendar months, and in captivity may attain almost 8 months; in nature males can certainly live almost 5 months, and in captivity may achieve 5½ months. However, only a very small proportion of the population is likely to achieve such extreme age.

8. Owing to the female's greater life-span, this sex should be the more dangerous vector of trypanosomiasis. But if it is proved that the female is less readily infected than the male, this may not be the case.

* * * * *

The following conclusions are based on tubed flies kept in White and Red Sections during the hot, dry weather.

9. The reason why wild flies evacuate the waterless reaches of a stream in the late dry season and concentrate by permanent pools is because failure to do so would result in their virtual extermination.[5]

10. Such virtual extermination would result from increases in the maximum temperature and maximum saturation deficit.

11. *a.* Over 10-day periods, average maximum temperatures of 88° F. (31° C.) are associated with an abnormally high mortality among a population composed of both sexes; but further analysis has shown that the male has a lower threshold for abnormal mortality than the female, being seriously affected by average maximum temperatures of only 84° F. (28·9° C.), when a comparable mortality amongst the females would not occur until 91° F. (32·8° C.).

b. Extermination of the females, and any surviving males, is associated with the mean maximum temperature reaching 93 to 95° F. (34–35° C.).

[5] Occasionally the vegetational insulation on a stream is so good that concentration by water is unnecessary.

12. Flies which spend their early life in a severe climate can tolerate higher maximum saturation deficits than those accustomed to a milder climate ; this prevents the determination of precise danger limits for this factor.

13. Females are more tolerant than males to high temperature and high saturation deficit.

14. This is believed to result in there being more females than males among the wild-fly population which survives the late dry season.

15. *a*. Flies from about 0 to 10 days old seem to be more susceptible to severe climatic conditions than rather older flies.

b. Flies from about 10 to 50 days old seem to be less susceptible than flies from about 50 to 90 days old.

16. Near the Nigerian northern limit for *G. palpalis*, even at 4 in. above a pool, the climate becomes sufficiently severe to cause abnormal mortality, which doubtless leads to the very low fly density associated with the end of the dry season.

17. The above results suggest that the partial clearing of riverine vegetation would effectively eradicate *G. palpalis* in all areas whose meteorological records show that one can be assured of getting maximum shade temperatures which will average 95° F. (35° C.) over a 10-day period. It is possible that an average maximum of 91° F. (32·8° C.) for two consecutive months might suffice.

10. FACTORS AFFECTING THE SEASONAL FLUCTUATIONS IN FLY DENSITY.

From the findings described in the preceding sections, it is believed that for the first time an insight can be obtained into the mechanism responsible for the well-defined annual cycle of seasonal fluctuations in the size of a population of *G. palpalis*. On p. 101 it was shown how closely the fly density was related to the evaporation rate. Now that the humidity and temperature components have been considered, the whole subject can be studied in greater detail.

The size of any tsetse population depends upon the reproduction rate and the length of the flies' life. The reproduction rate is related to the mean temperature of the environment, p. 109, not to the humidity (Jackson, 1949) ; the length of life is related to the maximum temperature, p. 129, and to the humidity, pp. 116 and 129.

An attempt has been made in fig. 14 to represent these factors graphically.

Fig. 14(A) shows the average monthly fly density for the main fly-round for the first four years of the investigation, and requires no comment at this point.

Fig. 14(B) is a graphical representation of the data given in Table X (p. 115). The average expectation of female life for each month's catch is shown by the length of the horizontal columns. Since, for example, flies caught in November may expect to live for an average of 64 days, those caught at the beginning of November can expect to survive until early January, whereas those caught at the end of November can expect to survive until early February : from early January to early February the number of November flies is steadily decreasing, which is suggested by the sloping end of the column. In this fashion the average expectation of female life for each of the twelve months has been represented. In the diagram, by following down the vertical columns, it is possible to count the number of monthly components which make up the population for any

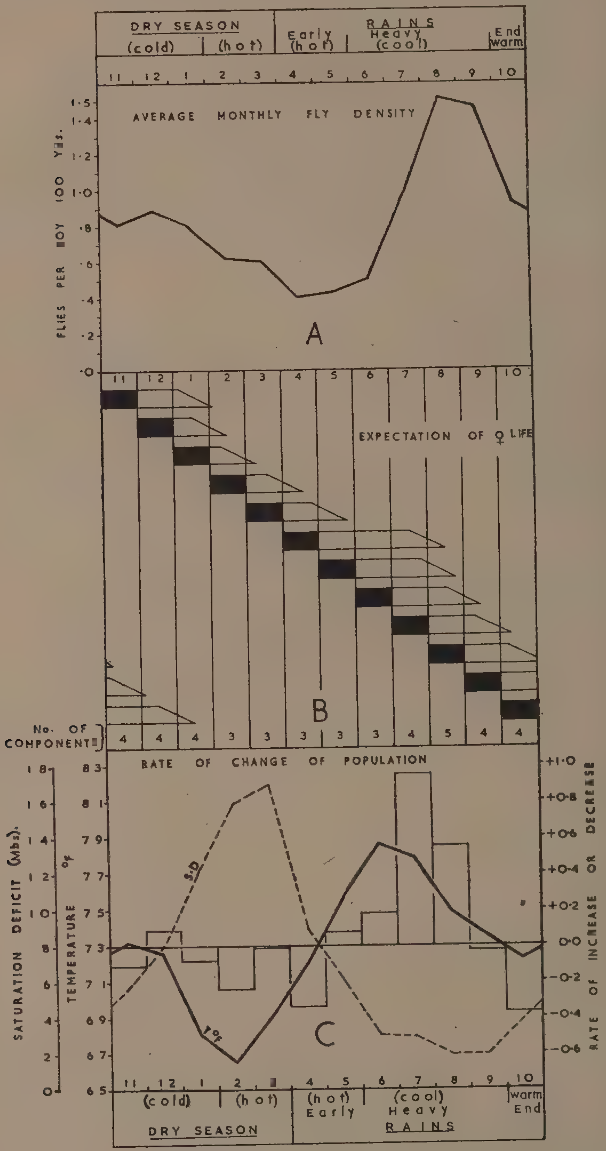


Fig. 14.—Some factors affecting the seasonal fluctuations in fly density during the first four years.

A. The average monthly fly density.

B. The average monthly expectation of female life.

C. The rate of increase or decrease, from month to month, in the average fly population (columns); the mean monthly saturation deficit (broken line); also, the mean temperature of 2 months before, which reflects the reproduction rate (continuous line).

month, and therefore to estimate any build-up or decrease that may be taking place in the fly community.

In fig. 14(C), the rate of increase or decrease in the fly population is shown by columns against the month in which the change became apparent. This figure has been obtained by the following method: If X is the population of one month, and Y the population of the next month, then $\frac{Y - X}{X}$ = rate of increase or decrease in month Y.

As the rate of reproduction is affected by the mean temperature, this factor has been plotted on fig. 14(C). But since any alteration in the mean temperature must first affect the gestation period and then the duration of pupal life, any such change cannot affect the size of the adult population for some considerable time. The mean monthly temperature has, therefore, been plotted two months after its occurrence, i.e., against the month whose population it is believed to have influenced. It is suggested that this mean temperature curve is a direct reflection of the reproduction rate. Lest this post-dating of temperature confuse the reader as to the real time of the seasons, these have been recorded in writing on the graph.

Since the longevity of the fly is influenced by humidity, the mean monthly saturation deficit has been shown (interrupted line) on fig. 14(C); it has been plotted against the month in which it occurred, because conditions unfavourable to longevity are likely to affect the size of the population fairly soon. Maximum temperature has not been shown, because it can only affect longevity between mid-February and the end of April.

Both the mean monthly temperature and saturation deficit data have been taken from the composite climate at 4 ft. above ground-level.

It will be seen that on the temperature scale the 73° F. (22·8° C.) point, and on the saturation deficit scale the 8 mb. (6 mm.) point, have been made to coincide with the zero line for rate of increase or decrease; this is because it has been found, not from this set of data alone, that these figures are near the critical turning point: Temperatures below 73° F. result in a subsequent decrease in population, and those above in a subsequent increase. Similarly, saturation deficits appreciably above 8 mb. are associated with population decrease and those below with population increase—except at very low saturation deficits, below 2 mb., when some adverse factor leads to a high mortality amongst flies, see p. 121, and hence to a decrease.

Let us now examine fig. 14(A) in the light of the information contained in fig. 14(B) and (C). The year will be divided into 4 periods.

A. *November-December* (Early Dry Season).

This is a period with little variation in the population.

It will be seen from (B) that the population of each of these months has 4 monthly components; the medium saturation deficits of this period permit the high expectation of life of the October flies.

The reproduction rate, as a result of the median mean temperatures of September and October, is average.

Thus in this period, the median reproduction rate and median longevity lead to the maintenance of the population, at a median level.

B. *January to April* (Mid-dry Season to Start of Rains).

This is a period of a great decrease in the population. (*N.B.*—In March the decrease is masked by an influx of stranger flies into Red Section (p. 101 and fig. 6).)

From (B) it can be seen that each of these months, except January, has only 3 monthly components in its population; the expectation of life, particularly of January flies, has been severely curtailed by the lethal maximum temperatures of the ensuing months (see p. 127), and by very high saturation deficits.

The reproduction rate has been greatly lowered in January, February and March by the low mean temperatures of November, December and January (C).

Thus in this period a greatly reduced longevity combined with some months in which the rate of reproduction is very seriously retarded, results in the reduction of the fly population to its minimum in April.

C. *May–August* (Early to Heavy Rains).

This is a period of colossal increase, leading to the maximum population in August.

From (B) it will be seen that, whereas May and June have only 3 monthly components, July has 4, and August has 5; this increase is due to the great expectation of life of the April, and, to a lesser extent, of the May flies. No dangerously high maximum temperatures occur and the saturation deficit favours long life except at the very end of the period.

The reproduction rate, too, becomes maximal, due to the very high mean temperatures of March, April, May and June.

Thus in this period the combination of maximal longevity with a maximal rate of reproduction leads to a maximal fly population in August.

D. *September–October* (Heavy Rains to End of Wet Season).

This is a period when the population drops from the peak to a median level.

From (B) it can be seen that there are now only four monthly components in the population. The expectation of life has been falling steadily throughout the rains; this fall may be associated with the very low saturation deficits of August and September, which are believed to cause abnormal mortality. Certain it is that when the saturation deficit rises in October the expectation of life increases sharply.

The rate of reproduction has been falling considerably as the mean temperature falls during the heavy rains.

Thus in this period the combination of reduced longevity with a reduced rate of reproduction leads to a decrease in the fly population, which brings it down to a median level.

* * * * *

From the foregoing it is apparent that the seasonal variations in the fly population are the result of the interplay of two factors—saturation deficit and mean temperature. When the former is favourable to longevity and the latter to the reproduction rate, then the fly population will increase. But if both are unfavourable, then the fly density will decrease; each year, a third factor—

maximum temperature—comes temporarily into play and accentuates the decrease.

Conclusions.

1. Within limits, the breeding rate increases at higher temperatures and decreases at lower temperatures. Mean monthly temperatures above 73° F. (22·8° C.) are associated with an increase in the tsetse population two months later, whereas mean temperatures below 73° F. are associated with subsequent population decrease.

2. *a.* Longevity is reduced at high and very low saturation deficits, but increased at intermediate saturation deficits. Mean monthly saturation deficits above 9 mb. (7 mm.) or below 2 mb. (1·5 mm.) are associated with a decrease in the tsetse population.

b. During two months of the year dangerously high maximum temperatures cause abnormally heavy mortalities, see p. 134, conclusions 11. *a.*

3. The decrease in the tsetse population throughout the dry season is due to a general decrease in longevity associated with rising saturation deficit, and a great decrease in the breeding rate associated with the cold dry season; in the late dry season longevity is further reduced by dangerously high maximum temperatures leading to a minimal tsetse population.

4. The great increase in the tsetse population in the first part of the rains is due to long life associated with intermediate saturation deficits and the absence of lethal maximum temperatures, combined with a greatly increased breeding rate associated with very high mean temperatures.

5. The decrease in the tsetse population at the end of the rains is due to decreased longevity associated with very low saturation deficit, combined with a reduced breeding rate associated with lower mean temperatures.

* * * * *

NOTE.

It is interesting to compare our longevity results for *G. palpalis* with those obtained by Nash (1936, p. 278) when working on *G. morsitans* and *G. tachinoides* at Gadau, N. Nigeria, where the climate is far hotter than at Kaduna, especially at the beginning and end of the dry season. He found that with these species, which are far less susceptible to low humidity than *G. palpalis*, there seems to be a close inverse relationship with the maximum temperature, i.e., as the temperature rises longevity decreases, as the temperature falls so longevity increases. He concluded that unless the maximum temperature is favourable, favourable humidity cannot increase the longevity.

Nevertheless the annual cycle for longevity has much in common with that now found for *G. palpalis*. Nash's cycle was as follows: The rains commence and maximum temperature falls; longevity increases and remains high throughout the rains, when the oldest individuals are found. The wet season ends, maximum temperature rises and longevity decreases. *The cold spell intervenes, longevity increases, and the average age of the flies becomes greatest.* The cold weather ends, the maximum temperature soars up and longevity decreases again to become minimal, remaining low until the new rains commence.

The only difference is that part which has been printed in italics. Instead of the more or less continuous decrease in longevity throughout the dry season which occurs with *G. palpalis* and is associated with falling humidity, in the case of *G. morsitans* and *G. tachinoides* the dry season decrease is interrupted in the cold season when these species, which are tolerant of medium-low humidity, achieve maximal *average* age ; but as soon as the hot weather returns (and evaporation becomes maximal) longevity again decreases, and, as with *G. palpalis*, becomes minimal in March or April.

PART III—THE FOOD FACTOR.

In order to study the nature of the tsetse's food supply and its seasonal availability, records were made of any hosts seen on the fly-rounds. These were traversed at regular intervals during 6 years, yielding observations on 288 days between the hours of 9 a.m. and 3 p.m.

The results are expressed as the number of *times* that a species was seen, not the number of individuals. (It is impossible to count a troop of baboons or monkeys in thick, evergreen vegetation.) Since our observations refer to the frequency of a species' presence, it should be remembered that a record of, for example, baboons seen on 10 occasions will represent a far greater number of hosts than Monitor lizards seen a similar number of times, since the latter species usually occurs singly.

Owing to the scarcity of game, which is typical of *G. palpalis* streams in this region, it has been impossible to make yearly comparisons of host abundance ; instead the data have had to be grouped for 6 years.

The following is a list of the hosts available, arranged in a descending order of frequency as determined from the second column of Table XV:

1st, Monitor lizard . .	*Varanus niloticus niloticus* and *exanthematicus.*
2nd, Baboon . . .	*Papio anubis choras.*
3rd, Monkey . . .	*Erythrocebus patas* and *Cercopithecus aethiops sabaeus.*
4th, Duiker . . .	*Sylvicapra grimmi coronata* and *Cephalophus rufilatus.*
5th, Cattle	
6th, Harnessed antelope .	*Tragelaphus scriptus scriptus.*
7th, Wart hog . . .	*Phachochoerus africanus.*
8th, Roan antelope . .	*Hippotragus equinus gambianus.*
9th, Water buck . . .	*Kobus defassa unctuosus.*

Table XV also indicates the seasonal abundance of each species.

In Table XVI the frequency of the appearance of the different species in the five-colour sections is shown ; in this table the numbers have had to be compensated to allow for variations in the lengths of the sections.

The last three species on the list occur so rarely that they may be ignored, as can be seen from Table XV, 2nd column. Man has been omitted from the list because, as will be seen from Table XVI, he virtually only occurs at one point on the 2400 yards of fly-round—the point where the trade route crosses the stream at the junction of Red and White Sections ; admittedly, at that point he is an important host.

The importance of the six relatively common species to the flies of each Colour Section is best assessed from Table XVI.

Green Section.—In this section, *G. palpalis* probably feeds mainly on baboons and duiker, and possibly on monkeys. We have no definite evidence that this tsetse does feed on baboons, but it almost certainly does so ; we know that *G. morsitans* favours this host in the Gambia (Nash, 1948*a*). Monkeys are less likely to be important because of their arboreal habits and speed of movement, which would make them restless, if not dangerous hosts.

TABLE XV.—*To show the seasonal availability of the different hosts.*

(The number of times each species has been seen during 6 years—for the whole period and by months.)

Species.	Total number of times seen.	Number of times seen in each month.											
		11.	12.	1.	2.	3.	4.	5.	6.	7.	8.	9.	10.
Monitor lizard . .	185	19	20	11	11	7	17	22	21	22	12	8	15
Baboon . . .	74	6	2	10	9	11	13	7	2	0	2	7	5
Monkey . . .	56	5	7	3	4	2	7	3	8	2	3	5	7
Duiker . . .	51	1	2	5	14	11	3	7	5	2	1	0	0
Cattle . . .	38	1	0	2	10	5	6	5	8	0	0	0	1
Harnessed antelope .	13	0	2	2	2	2	1	1	1	2	0	0	0
Wart hog . .	4	0	0	0	1	0	0	0	2	1	0	0	0
Roan antelope . .	2	0	0	0	0	0	0	1	0	0	1	0	0
Water buck . .	1	0	0	0	0	0	0	1	0	0	0	0	0
All species . .	424	32	33	33	51	38	47	47	47	29	19	20	28
		Dry season.					Wet season.						

TABLE XVI.—*To show the sectional availability of the different hosts.*

(The number of times each species has been seen during 6 years in the different colour sections. (*N.B.*—Numbers have been compensated to allow for variations in lengths of sections.))

Species.	Number of times seen in each colour section.				
	Green.	Red.	White.	Blue.	Yellow.
Monitor lizard . .	4	44	11	8	8
Baboon . . .	16	6	9	12	12
Monkey . . .	21	1	6	11	12
Duiker . . .	8	2	11	8	11
Cattle . . .	2	8	5	0	2
Harnessed antelope .	1	0	3	5	1
Wart hog . .	1	1	0	1	1
Roan antelope . .	0	1	0	0	1
Water buck . .	0	0	1	0	0
Man . . .	3	13	14	0	4

Red Section.—In this section Monitor lizards must be a very important source of food. Cattle are seasonally important, as the Fulani often graze their herds along the stream-edge between February and June (Table XV). Man is important to those flies that concentrate at the end of the section near the ford. Duiker are very rarely seen, presumably because the riverine vegetation is too thin to afford cover during the day-time, but the abundance of spoor suggests that they must visit the area at night.

White Section.—The largest range of choice occurs in this section, since in addition to the first five species listed, man forms an additional host at the ford.

Blue and Yellow Sections.—In both these sections the choice of hosts is virtually limited to baboon, duiker, Monitor lizards and possibly monkeys.

Since the greatest fly density occurs in the Green and Yellow Sections, it may be concluded that *G. palpalis* can thrive on a diet of only baboons, duiker, Monitor lizards and possibly monkeys; further, that medium and larger species of game are unnecessary.

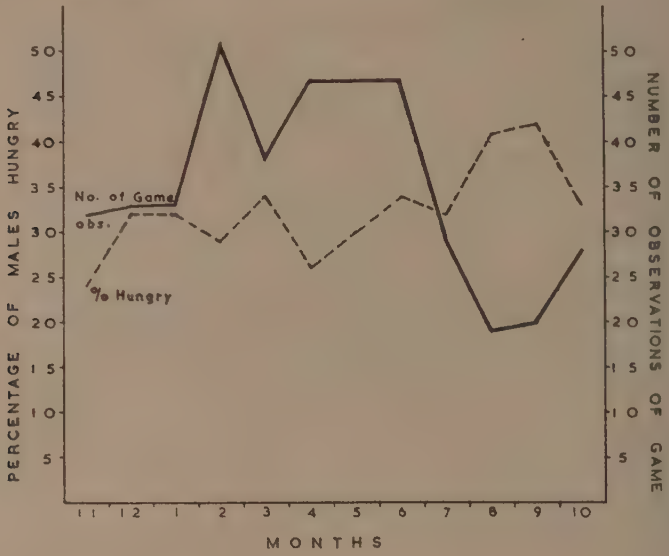


Fig. 15.—The season of hunger.

(As indicated by the number of observations of game, and the percentage of old males that were hungry, for each month of the year, based on 6 years' records.)

It is interesting to note in Table XV that Monitor lizards are infrequently seen in the very dry months—January to March; possibly they take shelter in holes in the banks from the desiccating conditions: they are also seldom seen in the height of the rains, August and September, when the stream is often flooded. Baboons become very scarce in the first three months of the heavy rains, June to August, and are commonest in the dry season, January to April. Duikers are rarely seen in the long grass season, July to December, but records of spoor show that they are only really scarce during November and December.

It will be noted from the frequency of observations for all species combined, given at the bottom of Table XV, that very few hosts are seen in August and September, suggesting that the height of the heavy rains may be a period when tsetse suffer from hunger: these data are shown graphically on fig. 15, continuous line. In support, data from an entirely different source are also shown—namely the percentage out of 8000 old, non-teneral male tsetse that were found to be hungry—interrupted line. (*N.B.* The simple hunger-staging system used was that described by Nash, 1937, p. 109). Clearly the tsetse were considerably hungrier in August and September than at any other time of year, which agrees with the dearth of hosts seen at that season. Presumably the inundation of much of the riverine vegetation causes many of the host species to move temporarily into the adjacent savannah. This temporary hunger cannot be due solely to the concealment by high grass of game feeding in the adjacent savannah, because the grass does not reach its maximum height until October and is not burnt until December or January, whereas excessive fly hunger has ended by October, when inundation ceases as the rains peter out.

The great decrease in fly density which starts in September, p. 138, may be partly caused by hunger during the height of the heavy rains.

Conclusions.

1. *G. palpalis* can thrive on a diet of only baboon, duiker, Monitor lizard and possibly monkey blood ; the blood of the medium and larger species of game in unnesessary.

2. *a.* The fly experiences definite hunger at the height of the heavy rains, when inundation of the fringing forest is believed to drive most of the hosts into the adjacent savannah.

b. This temporary separation of the fly from its hosts may contribute to the decrease in the size of the tsetse population that takes place towards the end of the rains.

PART IV—THE VEGETATION FACTOR.

1. INTRODUCTION.

We have been greatly helped in the work described in this part of the paper by a vegetational survey of the fly-round sections, which Mr. R. W. J. Keay and members of the Ibadan Forest School very kindly undertook on our behalf. With this invaluable basis behind us we have, however, tended to interpret our findings in relation to the configuration of the vegetation rather than to its species composition.

A study of the relationship between different types of riverine vegetation and *G. palpalis* entails a detailed investigation of the fly density both in the colour-sections and in their component, 100 yards long subsections. Having found from the fly density figures which are the most popular sections, it is then necessary to ascertain whether this attractiveness is purely seasonal or whether it extends throughout the year : in the latter eventuality it may be assumed that the ideal vegetation type has been discovered, providing that this continuous popularity is not due to some other cause such as a permanent food supply at a road crossing. Conversely, persistently unattractive sections are likely to indicate an unattractive form of vegetation, providing no other adverse factor is discernible.

The findings for this part of the paper are based on 16,766 *G. palpalis* caught over 6 years.

2. THE ATTRACTIVENESS OF THE FIVE COLOUR-SECTIONS, BY YEARS AND BY SEASONS.

(a) Attractiveness by Years.

In Table XVII, owing to the different lengths of the colour-sections, the total number of flies caught in each have been expressed as flies, per 100 yards, per annum. The letters A, B, C, D, and E in the first column denote the order of severity of the different dry seasons as given on p. 90, " A " being the most severe, and " E " the least.

TABLE XVII.—*The relative attractiveness to* G. palpalis *of the colour-sections for each of* 6 *years.*

(Expressed as flies, per 100 yards, per annum.)

Year.	Green.	Red.	White.	Blue.	Yellow.
1st. A	—	115	81	46	198
2nd. B	262	56	72	22	121
3rd. C	197	58	72	51	183
4th. E	256	82	132	129	418
5th. D	168	51	105	105	366
6th. B	300	64	98	93	320
Total	1183*	426	560	446	1,606

* This total covers only 5 years.

It will be seen from the bottom line of the table that the greatest number of flies was caught in Yellow Section ; however, Green Section's total covers only 5 years. Unfortunately, data for Green are available for only the last four months of the 1st biological year, but during those months Green supported a much higher population than Yellow :

Month.	Green section.	Yellow section.
July, 1945	192 flies	2 flies
August, 1945	152 ,,	15 ,,
September, 1945	121 ,,	24 ,,
October, 1945	100 ,,	48 ,,
Total	565 flies	89 flies

It therefore seems fair to assume that had the full data for the 1st year been available, Green would have produced at least as many flies as Yellow over the 6 years. It may be concluded that Green and Yellow Sections are some three times more attractive than Red, White or Blue.

(b) Attractiveness by Seasons.

Having discovered the most popular colour-sections, the next step is to see whether their attractiveness is purely seasonal or if it extends throughout the year. The annual data given in Table XVII have therefore been subdivided into four periods of equal length which approximately cover the five seasons described on pp. 74–75. These four, three-monthly periods, have been designated as follows in Table XVIII, and cover the following seasons :

1st half dry = November to January. The Cold Dry Season.
2nd half dry = February to April. The Hot Season—mainly dry, but rain may fall in April.
1st half wet = May to July. The Early to Heavy Rains.
2nd half wet = August to October. The heavy Rains to End of Rains.

The relative *seasonal* attractiveness of each of the five colour-sections has been assessed and described in terms of occupying 1st, 2nd, 3rd, 4th or 5th place in order of attractiveness. See columns 3 to 7 of Table XVIII, where each colour-section is recorded by its initial letter in the place which it has earned. When two sections tie for a place their initials are shown together, midway between the appropriate columns. The letters A to E in the first column again refer to the severity of the dry season.

TABLE XVIII.—*The order of attractiveness of each colour section for each of the four seasons, for each of the six years.*

(Based on the flies caught per 100 yards, per season of 3 months.)

		Order of attractiveness.				
Year.	Season.	1st.	2nd.	3rd.	4th.	5th.
1st. A	1st half Dry	G ?	Y	W	R	B
	2nd half Dry	G ?	Y	R	WB	
	1st half Wet	G ?	R	W	B	Y*
	2nd half Wet	G	R	W	Y	B
2nd. B	1st half Dry	G	YW		R	B
	2nd half Dry	G	Y	R	W	B
	1st half Wet	G	Y	R	W	B
	2nd half Wet	G	Y	W	R	B
3rd. C	1st half Dry†	G	Y	W	RB	
	2nd half Dry	G	Y	W	R	B
	1st half Wet	G	Y	W	R	B
	2nd half Wet	Y	G	W	B	R
4th. E	1st half Dry	Y	G	W	B	R
	2nd half Dry	Y	G	W	BR	
	1st half Wet	Y	G	B	W	R
	2nd half Wet	Y	G	B	W	R
5th. D	1st half Dry	Y	G	W	B	R
	2nd half Dry	Y	G	W	B	R
	1st half Wet	Y	B	G	W	R
	2nd half Wet	Y	G	B	W	R
6th. B	1st half Dry	Y	G	W	B	R
	2nd half Dry	Y	G	RW		B
	1st half Wet	G	Y	B	R	W
	2nd half Wet	G	Y	B	W	R

* Yellow Section had been gutted by fire on 29/iii/45.
† Fire-breaks instituted.

The Green and Yellow Colour-sections.

Table XVIII suggests that in the severe first three years Green held first place, and Yellow second place, apart from a temporary interruption at the end of the 1st year, when Yellow fell back to fifth place after being gutted by fire. However, in the very mild 4th and 5th years, and until the middle of the 6th year, Yellow held first place and Green was almost always second ; but in the latter half of the 6th year Yellow fell back to second place, probably as a result of the exceptional severity of the late dry season.

Yellow Section is not as safe as Green in very severe years, and cannot be considered a permanent habitat because, as happened in the 1st year, it can be gutted by fire with disastrous results to the fly population. This can be seen from the following figures : In March, 1945, the number of flies in Yellow was reduced from 19 to 1, whereas on the Main Fly-Round the ordinary seasonal drop was only from 89 to 46. Even in the following July, Yellow yielded only 2 flies, see p. 144.

Yellow might have been gutted by fire in subsequent years, had we not felt compelled to cut fire-breaks along the whole round at the beginning of the 3rd and following years, lest we find ourselves with a newly constructed field station, but no flies. In retrospect, we feel that Blue and Yellow Sections, with their lack of peripheral creeper curtain and presence of intrusive grass, were the only sections to benefit by the fire-breaks ; the exclusion of fire probably allowed the vegetation to become thicker, which would account for the increased favourability of these two sections in the severe 6th year as against the equally severe 2nd year.

The Main Fly-round Colour-sections.

Red.—In the second half of the dry season in severe years (1st, 2nd and 6th), Red, at third place, is always the most popular section of the main fly-round : but in mild years (4th and 5th) it gives way to White or even Blue Section. In view of its efficiency as a late dry season sanctuary it should be classed as a permanent habitat, since it can support a small fly population throughout *all* seasons of *all* years.

White.—In the first half of the dry season, White, at third place, is always the most popular section of the main fly-round. This is also true for the second half of the dry season in mild years (3rd, 4th and 5th), but not in severe years (1st, 2nd and 6th), when it drops back to fourth place, having given way to Red. It could not be classed as a permanent habitat.

Blue.—In the second half of the dry season of the more severe years (1st, 2nd, 3rd and 6th), Blue, at fifth place, is the least popular of all sections ; but in very mild years (4th and 5th) it is less unattractive, resulting in a great increase in popularity in the first half of the rains. (In the 6th year the presence of a fire-break may have helped the flies in this section, which, like Yellow, was very susceptible to fire damage). Blue could not possibly be classed as a permanent habitat.

3. THE SEASONAL ATTRACTIVENESS OF THE SUBSECTIONS OVER SIX YEARS, IN RELATION TO VEGETATION AND OTHER FACTORS.

Hitherto we have dealt with colour-sections as our units, but now propose to study the attractiveness of each of the 100 yards long subsections into which the Red, White and Blue colour-sections of the main fly-round were subdivided. It will be seen in Table XIX, A. that the subsections are denoted as 0–1, 1–2, etc.; these are abbreviations for 0–100, 100–200 yards, etc.

TABLE XIX.—*The relative attractiveness of the fly-round subsections.*

(Over 6 years the average number of flies, per season, per subsection of 100 yards—A; this number also shown as a percentage of each subsection's average yearly catch to facilitate seasonal comparisons within each subsection—B.)

MAIN FLY-ROUND, BY SUBSECTIONS.

A. Flies.

Season.	Green section.	Red section.										White section.					Blue section.			Yellow section.
		0–1.	1–2.	2–3.	3–4.	4–5.	5–6.	6–7.	7–8.	8–9.	9–10.	10–11.	11–12.	12–13.	13–14.	14–15.	15–16.	16–17.	17–18.	
												Ford								
1st half Dry .	67*	7	5	10	11	22	15	15	17	17	42	17	19	50	42	32	18	15	11	77
2nd half Dry.	45*	4	3	6	20	20	16	13	12	11	27	9	6	13	14	10	5	7	5	42
1st half Wet .	48*	3	4	9	14	22	14	15	15	16	22	9	7	13	19	22	10	18	18	46
2nd half Wet .	76*	19	17	22	25	35	35	32	28	27	45	29	24	36	50	47	36	43	38	103
Average yearly catch . .	236*	33	29	47	70	99	80	75	72	71	136	64	56	112	125	111	69	83	72	268

B. Percentages.

Season.	Green section.	0–1.	1–2.	2–3.	3–4.	4–5.	5–6.	6–7.	7–8.	8–9.	9–10.	10–11.	11–12.	12–13.	13–14.	14–15.	15–16.	16–17.	17–18.	Yellow section.
1st half Dry .	28	21	17	21	16	22	19	20	24	24	31	27	34	45	34	29	26	18	15	29
2nd half Dry .	19	12	10	13	29	20	20	17	17	15	20	14	11	12	11	9	7	8	7	16
1st half Wet .	20	9	14	19	20	22	18	20	21	23	16	14	12	12	15	20	14	22	25	17
2nd half Wet .	32†	58	59	47	36†	35†	44	43	39	38	33†	45	43	32	40	42	52	52	53	38

* Average based on last 5 years only. † Permanent habitats.

The 300 yards long Green and Yellow subsidiary fly-rounds were not subdivided on the ground into subsections, but to make comparison possible their fly totals have been divided by 3, so that all figures given in Table XIX, A. refer to the average number of flies caught over 6 years, per season, *per* 100 *yards*. The average yearly catch is shown along the bottom line. In Part B of this table the proportion of the average yearly catch which occurred in each season is expressed as a percentage.

In an ideal permanent habitat the population should vary little throughout the year, so that theoretically 25 per cent. of the average yearly catch should occur in each of the four seasons. The subsection which approaches this standard most closely is considered by us to be the nearest to the *ideal* permanent habitat, and therefore, even though its average yearly catch may be low, it is much more important to the fly community than some other subsections which produce far more flies, but only at certain favourable times of year.

From Part A of the table it is obvious that Green and Yellow support a far higher fly density per 100 yards than any 100-yard-long subsection. From Part B it can be seen that whereas at no season does Green deviate from 25 per cent. by more than 7 per cent., the deviation in Yellow is up to 13 per cent. Obviously Green forms a nearly perfect, major permanent habitat.

The Green Section.

The reason for the perennial attractiveness of the Green Section will now be studied. It cannot be due to an abnormal number of hosts, see Table XVI, nor can it be due to the formation of a microclimate within a deeply-cut stream-bed, as the banks are only 3–4 ft. high. Nor can it be due to any remarkable persistence of surface water since for much of the dry season the stream-bed is waterless, apart from one tiny puddle which only dries up for one or two months.

The following indicators, however, suggest that the water-table must remain high throughout the dry season: The fringing forest is darkly evergreen in appearance; the palm *Raphia sudanica* is exceedingly abundant; a narrow strip of moist savannah woodland frequently occurs along the margin of the forest, and a small area of treeless marsh borders the forest near the start of this section. There can be no suggestion of swamp forest, the country being far too well drained, but the vegetation does indicate the presence of sub-soil water at no great depth.

On the east side—the side against which fierce fires will be driven by the north-east Harmattan wind—the edge of the forest is sharply defined; in places it presents a vertical, fire-resistant creeper curtain, and in others a resistant wall of Raphia and evergreen shrubs (Plate I). On the safe west side the wall is not vertical, the tangle tumbling down in steps to the ground; in some places, however, the forest merges into a thick, low woodland of *Uapaca somon*, beneath which grass is largely suppressed, thus affording *G. palpalis* feeding grounds which are sheltered in the dry season, and provide good visibility even in the long grass season. An example of this type of woodland is shown in Plate III, fig. 2.

A very important feature is the indented nature of the forest edge, which leads to the formation of small bays surrounded on three sides by forest, these can be inspected by *G. palpalis* for hosts without the fly ever having to leave its habitat (Plate III, fig. 1).

The average width of the fringing forest is 97 yds. Isolated trees, 60–70 ft. high, emerge from a fairly uniform canopy 40–50 ft. high, in which the Raphia palm is dominant. Beneath this canopy is an understorey which ranges from clumps of impenetrable evergreen thicket, or tunnels between the bases of the Raphia, or low umbrella-like creeper tangles, to small open patches under high shade where there is little undergrowth (Plate II); a great variety of resting haunts and feeding grounds occur *within* the forest.

The Green Section is a major permanent habitat.

The Yellow Section.

This section is really a favourable *temporary* habitat, a fact which is largely masked in Table XIX by the unexpectedly large numbers of flies caught in the late dry season and early rains; however, some 50 yds. below Yellow there is a semi-permanent habitat, of a very different vegetation type, from which Yellow draws it population in the late dry season.

The stream-bed of Yellow is shallow, and may be waterless for four months of the year (Table IV, p. 90). Raphia palm is virtually absent, and the general impression is that of mixed-deciduous forest, on a well-drained soil, with a tendency for any evergreen species to be confined to the vicinity of the stream —there is nothing to suggest a high water-table.

The average width of the forest is 65 yds. Emergents, up to 70 ft. in height tower above the general vegetation. There is an occasional small thicket

(Plate V, fig. 2), but no lateral vegetational curtain to protect the forest from wind and fire ; however, vertical insulation against the sun is provided by a canopy, 15–20 ft. high, which, starting in the adjacent woodland, becomes denser near the stream owing to the presence of climbers.

As the canopy becomes heavier the grass disappears and is replaced by low herbs (Plate V, fig. 1), but in places an understorey of small tree seedlings forms a light shrubbery. This combination of good visibility under high shade provides excellent tsetse feeding-grounds, particularly for use in the second half of the rains, when conditions in denser types of forest are too humid, and the grass outside is too high for food to be easily found ; good visibility is also operative in favour of Yellow in the early dry season, before the grass is burnt.

Excellent breeding sites are provided by the forest floor, and under the large horizontal trunks of lianes (Plate V, fig. 1) and small trees such as *Olax* sp. which have an umbrella-like growth form ; however, our puparia rounds show that larviposition ceases in the late dry season, presumably owing to the lack of lateral vegetational insulation.

In several places the woodland savannah penetrates to the stream-bank, and isolated grassy glades occur within the forest. It is not surprising therefore that when the area happens to be burnt late, the flames sweep into the forest, and ignite dead creeper tangles in the canopy.

It may be concluded that an extensive low shade canopy with little undergrowth, but occasional thickets, provides ideal conditions for *G. palpalis* in the heavy rains and throughout the long grass season, but is inadequate in the hot late dry season, owing to the absence of lateral insulation. The vegetation of Yellow should be classed as forming a very favourable temporary habitat.

* * * * *

The subsections of the main fly-round will now be dealt with.

The Red Section.

This 1000 yds. long stretch of stream is characterised by fringing forest which is extremely narrow but usually well insulated, by the existence of some pools which never dry up, and by a stream-bed which for the most part runs below well-defined, steep banks.

The width across the riverine vegetation may be as little as 5–7 yds., but where the stream suddenly changes direction the fringing forest may fill the bend and be 25 to 30 yds. in width. Emergents, 35–40 ft. high, sometimes form a canopy over the tangle-cover which roofs over the stream.

On the north bank—the quarter from which bush fires come—the riverine vegetation has, in the course of years, been burnt back to such an extent that most of it grows out of the stream-bed. But on the sheltered southern side the forest frequently extends a little way out onto the bank, and occasionally merges into a very narrow strip of transitional woodland which produces sufficient canopy to restrict considerably the growth of grass (Plate III, fig. 2).

The fringing forest of Red Section has much in common with that of Green both as regards species-composition and general evergreen appearance ; but it is on a greatly reduced scale both as regards height and width, and almost entirely lacks the small open feeding grounds under high shade which characterise the Green Section.

Turning now to Table XIX, so that a detailed analysis can be made of the subsections, it will be seen that 0–1 and 1–2 support the lowest fly density of any subsections, and that the bulk of the flies caught here are taken in the second half of the wet season—a fact which suggests that conditions must be almost intolerable except at the most humid time of year. This is readily understandable: the banks are ill-defined and shallow, preventing the formation of pockets of cool, humid air in the dry season. The riverine vegetation is only 5 to 7 yds. wide and can be seen through easily; its roots grow entirely within the stream-bed and so block the tsetse's flight-line (Plate VII). Pools of water persist in all but the most severe years, but can be of little use to the tsetse in the dry season, as ready approach could only be made by flying through the hot savannah.

Conditions improve in Subsection 2–3 with a uniformly high canopy throwing a line of shade over the stream-bed, which here offers a free flight-line, but the forest is still exceedingly thin. These first three subsections form unfavourable temporary habitats.

From 3–4 the riverine vegetation tends to spread out on to the top of the south bank; although still very narrow it cannot be seen through. The stream-bed now becomes well defined, with banks about 7 ft. deep and a channel that is only 11 ft. wide; a good flight-line is available, as well as a deep-cut channel for the retention of the microclimate; during six years the water never dried up entirely. As can be seen from Table XIX, A, the fly density here is considerably greater, and from part B it is clear that this subsection forms an excellent late dry season sanctuary; it can be classed as a minor permanent habitat, since in none of the four seasons does the percentage deviate by more than 11 from the expected figure of 25.

From 4–5 conditions are very similar to those just described for 3–4, but owing to forested bends the vegetation is considerably wider and there is an excellent little feeding ground at a point where shelving banks permit game to drink and Fulani cattle to be watered in the dry season. This crossing-place covers an area of some 300 sq. yds. under high shade with no undergrowth, yet only 20 ft. upstream there is a permanent pool under sheer banks which are 10 ft. high and 11 ft. across (Plate IV). Hence, *G. palpalis* has perfect microclimatic conditions for the dry season on the edge of an ideal feeding-ground. This subsection can be classified as a good minor permanent habitat: in no season is the deviation from 25 per cent. greater than 10 (see Table XIX, B).

Along the next four subsections, 5–9, the width of the fringing forest remains narrow, except for a few forested bends, but it is very dense and can rarely be seen through; the stream-bed remains deep and narrow. Were it not for the complete absence of feeding-grounds density would doubtless be higher, and these subsections would probably qualify as minor permanent habitats. They are certainly valuable as sanctuaries in the second half of the dry season in all but the most severe years, when some of them, especially 8–9, may dry up.

Subsection 9–10 supports the highest fly density of Red Section, and is obviously an important permanent habitat; in no season is the deviation from 25 per cent. greater than 9. Its popularity is due to a clear flight-line between high banks, a pool of water that only dried up in the most extreme 1st year, and to the presence of a feeding-ground at either end. Near 9 there is a glade in a forested bend with good visibility under high shade, and at 10 there is the trade-route crossing over the stream.

This study of Red Section has enabled us to draw up lists of unfavourable and favourable features which should be looked for when assessing the value of a stream as a permanent habitat for *G. palpalis.*

Unfavourable Factors :

1. Very narrow fringing forest that can be seen through, and hence provides inefficient vegetational insulation (Plate VII, fig. 1).
2. Fringing forest which grows out of the stream-bed, if by so doing it will block the whole channel and hence the tsetse's flight-line (Plate VII, fig. 2).
3. A lack of feeding grounds, due either to the absence of drinking places or fords, or to the absence of a high canopy which is capable of suppressing the undergrowth of the fringing forest or the grass of the adjacent savannah.
4. Shallow banks which are incapable of protecting the microclimate of the stream-bed from dissipation by wind (Plate VII, fig. 2).

Favourable Factors :

1. A high, dense peripheral curtain of evergreen creepers and shrubs which can keep out wind and fire (Plate I).
2. A clear flight-line along the stream so that the fly can wander in search of food without leaving its ecoclimate (Plate IV, fig. 1).
3. An abundance of potential feeding-grounds with good visibility which can be readily inspected by the fly, without leaving its ecoclimate (Plate IV, fig. 2).
4. Sheer, steep banks to the stream (Plate IV, fig. 1).
5. The presence of permanent pools of water which ameliorate the climate, and attract hosts (Plate IV, fig. 1).

The White Section.

The fringing forest of this section is very different from that of Red, being much wider and of a much drier type. There are no Raphia palms. The records of the number of months in which the stream-bed was dry (Table IV, p. 90) suggest a porous soil with poor powers of water retention. In three of the six years Subsection 11–12 never held water, not even in the rains.

White Section should be dealt with in two parts owing to a vegetational difference that is believed to be of vital importance to *G. palpalis*, viz., *the first three subsections contain no thickets, whereas the last two are composed mainly of thickets.*

The vegetation of the first three subsections, 10–13, is characterised by a closed canopy 40–50 ft. high with emergents up to 80 ft. high, and an understorey of small erect shrubs and herbs. There is no peripheral curtain ; in places one can see right through the fringing forest, even though its average width is 50 yds. (Plate VI, fig. 1). The complete lack of lateral vegetational insulation and the shallow stream banks suggest that these subsections should be most unfavourable in the late dry season and early rains before re-population takes place, whereas the excellent visibility under high shade suggests a perfect feeding-ground and temporary habitat at milder times of year. Reference to Table XIX, A, shows that in fact the first two subsections do support a very low fly density, but that 12–13 is well-populated, which is only to be expected as it borders on 13–14, which is full of thickets from which the flies come out to feed. Reference to Table XIX, B, confirms that the popularity of these subsections is much greater in the second half of the wet season and first half of the dry season.

In the last two subsections, 13–14 and 14–15, the vegetation is very irregular, much of the land having been farmed in the past. Occasional relict trees, 70–80 ft. high, tower above a tangle of creeper and thickets, but are too widely spaced to produce a high canopy. Beneath these are occasional smaller trees with crowns choked with tangle, producing undergrowth-free patches of heavy shade. Then there are high, dense mounds of thickets and an occasional grassy glade. In places a dense low tangle forms a tunnel through which the stream-bed runs. On the exposed north side the forest is bounded by a discontinuous and not too efficient wind-break of dense low thicket, but on the sheltered south side the thicket is continuous. The insulation in these subsections is not very effective because the thickets are not entirely evergreen. It is clear from Table XIX that in the absence of permanent pools or a high water table this type of irregular, mixed thicket with no canopy is quite incapable of effectively supporting a fly population in the second half of the dry season. However, such irregular vegetation is attractive under the milder conditions of the second half of the wet season and first half of the dry.

The lesson to be learned from a study of White Section is that in these latitudes an extensive area of high closed canopy with an understorey of small shrubs, but no peripheral curtain, is not really attractive to *G. palpalis*, even in the rains, unless there are dense thickets in the immediate vicinity.

The Blue Section.

The vegetation of this colour-section is even more irregular than the adjoining subsections of White, due to the fact that it was farmed more extensively being nearer to an old ruined town, and was possibly cultivated up to a later date. The vegetation is of a much more deciduous type than that of White.

There is no high, closed canopy—only an occasional giant, relict Kapok (*Ceiba pentandra*) or *Parkia oliveri*. In places there may be a light canopy produced by small-boled woodland trees, with grass greatly suppressed, which extends down to the stream, or there may be large glades of grass, or tongues of deciduous *Acacia ataxacantha* thicket running out at right angles from the stream (Plate VI, fig. 2). The stream may run through the open, or under a narrow canopy of *Milletia thorgii*, which is deciduous ; only occasionally does the channel pass through creeper tunnels, and even then, though the roof may be thick, the sides may be very thin or even absent. The banks of the stream are also unsuitable for the retention of microclimates, the exposed north bank often being only a few feet high, whereas the south bank may form a cliff some 15 ft. in height. There is no peripheral creeper curtain, in fact it is often impossible to demarcate the edge of the fringing forest. The absence of Raphia, the scarcity of *Syzgium guineense* and the deciduous nature of the vegetation all suggest a low water table, which is borne out by the fact that even in the mildest dry seasons this colour-section always dries up (Table IV, p. 90).

The irregularity of the conformation of Blue Section provides good feeding-grounds, and thickets that are adequate so long as they retain their leaves; one would therefore expect this well-drained area to be relatively attractive in the heavy rains, but most inhospitable in the hot dry weather. Reference to Table XIX shows that over half the flies caught in the year are taken in the second half of the rains, and that very few are taken in the hot, late dry season.

The lesson to be learned from the study of Blue Section is how important it is to *G. palpalis* to have *evergreen* vegetation and a well-defined, well-insulated habitat.

* * * * *

The reader may have been surprised that on the main fly-round, and in the second half of the dry season, there is so little difference between the average number of flies caught in permanent and temporary habitats, cf. 20 flies in the permanent habitat, 3–4, as against 14 flies in the temporary habitat, 13–14. But it must be remembered that whereas in the most severe years almost all the flies are caught in the permanent habitats, in the mild years there is a tendency for the process to be reversed, as was shown in Table VI, p. 97, cf. fly densities for Red and White in 1st and 4th years. It is these mild years which reduce the difference.

Table XIX, B, suggests that 4 places may certainly be considered to be permanent habitats, *see* daggers. Of these, only Green Section can attribute its continuous attractiveness to the vegetational factor alone. In the case of the others, there were contributory factors such as permanent pools, fords, high banks, etc.

4. CONCLUSIONS.

G. palpalis cannot tolerate a wide range of climatic conditions such as occur in the savannah belt; nevertheless, it has successfully penetrated deep into this huge zone, but at the cost of its freedom of movement, which is virtually restricted to the ecoclimate of the water courses or islands of forest. Under such conditions climate is undoubtedly a vital factor in the ecology of *G. palpalis*; but surface water and vegetation are key factors in the formation and retention of the ecoclimate upon which *G. palpalis* is dependent for survival.

Our concepts, based on the results from the fly-round stream and general observations in northern Nigeria, may be summarised under four headings:

(a) Characteristics of Major Permanent Habitats which are Independent of Surface Water.

The fringing forest must be extensive and predominantly evergreen in composition, which will probably depend on the presence of sub-soil water at no great depth.

On the exposed side the edge of the forest must be sharply defined, presenting a high wall of dense vegetation which will provide *lateral* insulation against wind and fire. There must also be a closed canopy which will provide *vertical* insulation against the sun. Within the forest there must be exceedingly dense thickets to offer additional shelter under extreme climatic conditions.

There must also be a wide variety of feeding-grounds for use at different times of year, ranging from deeply-shaded glades within the forest to intrusive bays of savannah, and strips of transitional woodland forming a canopy along the edge of the forest.

The combination of dense vegetation and open feeding-grounds under high shade is essential to the formation of a major permanent habitat for *G. palpalis*. (*N.B.*—Nash (1948*a*, p. 10) describes how in a certain area some of the impenetrable islands of forest were unwittingly made attractive to *G. palpalis* by introducing ginger farming to certain villages; the people cleared tongues into the impenetrable forest but left the tall trees standing, and so produced much needed fly feeding-grounds; only in these villages were tsetse and sleeping sickness common.)

In the ideal permanent habitat there should be such a diverse range of vegetation over a relatively small area that the fly can rest, feed or breed, at any season, without ever having to leave the narrow climatic range by which this species is limited.

Such major permanent habitats are rare in these latitudes.

(b) Characteristics of Minor Permanent Habitats which are Dependent upon Surface Water.

Minor permanent habitats of this type, characterised by a narrow fringe of forest, are very common in the northern part of Nigeria and throughout the hinterland of West Africa; upon them depend the survival of *G. palpalis* and the transmission of sleeping sickness.

In such habitats there must be an easily-accessible permanent pool of water, forming a microclimate whose retention is assured by steep stream banks and good vertical and lateral vegetational insulation. Within the forest ecoclimate there must also be potential feeding-grounds with good visibility under high shade. Unless a village draws its water from the permanent pools the fly population is likely to be very small, as good feeding-grounds providing a steady supply of wild hosts tend to be rare.

(c) Characteristics of Favourable Temporary Habitats.

Such habitats are characterised by an extensive closed canopy with suppressed grass or undergrowth (and hence good visibility), *combined* with the presence of thickets; there is no peripheral wind-break. The composition of neither the canopy nor the thickets need be evergreen, since these temporary habitats have insufficient lateral vegetational insulation to make them habitable in the dry season of severe years.

Favourable temporary habitats are of great value to the fly community in the heavy rains and early dry season. They provide extensive feeding- and breeding-grounds which can support a large tsetse population at a time when the minor permanent habitats may be too humid and relatively unattractive, due to the flooding of some of their internal feeding-grounds and to the height of the grass in the adjacent savannah.

(d) Characteristics of Unfavourable Temporary Habitats.

Such habitats may be of very different types. There is the type in which the vestigial forest is mainly evergreen, but so narrow that it gives inadequate lateral insulation; the stream-bed is shallow and choked with vegetation. Then there is the drier type in which the fringing forest is very wide, with low undergrowth and excellent vertical insulation, but no dense thickets and no lateral insulation. Lastly there is a very different type in which the fringing forest is extensive and ill-defined; it consists of much secondary thicket, which is deciduous and therefore valueless when it loses its leaves; there is no canopy to provide vertical insulation.

In all three types flies are only caught in appreciable numbers in the heavy rains and sometimes in the early dry season, but even then the numbers are relatively small.

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It would appear that in these latitudes *G. palpalis* must have vegetational insulation that is effective both laterally and vertically.

5. THE ECONOMIC IMPLICATIONS OF THE VEGETATIONAL FINDINGS.

For the large-scale eradication of *G. palpalis* and *G. tachinoides* in Northern Nigeria the method in use is that of "partial clearing." The tall, clean-boled trees are spared and all undergrowth and low-branching trees are felled, so as to permit the dissipation of the dry season ecoclimate by the Harmattan wind; by the end of the dry season the tsetse have been destroyed. A ruthless barrier clearing is introduced on the last mile of the stream system to prevent a wet season re-infestation of the partially cleared reaches from the uncleared end. The ruthless method is also employed in small protective clearings, which are designed to safeguard villages or stream-crossings and so break the man-fly contact at definite points (Nash, 1948*a*, pp. 21–23, and Plate IV, figs. 1, 2 and 3).

The initial costs of both partial and ruthless clearing are doubled by the necessity of piling and burning the trash over the stumps to reduce subsequent regeneration; even so, annual re-slashing is needed for many years. At the time of the initial clearing stumping can be undertaken, but the cost is prohibitive and serious erosion may result. In Nigeria the stage is being reached where so much time ought to be spent on supervising the re-slashing of some thousands of miles of cleared streams that there will be little staff left for new undertakings. The labour wage is now five times greater than it was before the war, so that there is also an urgent need to reduce the costs.

The conclusions given in the last section of this paper, combined with general observations over many years by the senior author, suggest the feasibility of an entirely new method of clearing which should be well worth a trial by those bodies which have staff and funds for experimental reclamation. If successful it would enormously reduce the initial costs of clearings directed against *G. palpalis* and abolish the need for maintenance.

The proposed method, which might be called "obstructive clearing," should be directed against that very common type of small stream insulated laterally by shrubs, scandents, and climbers, and vertically by the creeper-covered crowns of medium-sized trees which produce an overhead canopy, out of which rears an occasional emergent. It is suggested that the trees of the canopy should be felled so as to fall across the stream, but that the shrubs, thickets, creepers and giant emergents should all be spared. It is visualised that the crowns of the felled trees would rapidly become overgrown with creepers, the tsetse's flight-line would be blocked, and the overhead canopy destroyed; the fringing forest would have been reduced to a line of low, impenetrable tangle and thicket, out of which an occasional emergent would tower: it is believed that the final result would look somewhat like fig. 2 of Plate VI. The essence of the method would be to *obstruct* the flight of *G. palpalis*, and deny it the benefit of a canopy which provides vertical insulation against the sun. Such a method could probably be used on large-scale schemes, as well as for preventing access by tsetse to individual village watering places. It would probably be many years before young trees had forced their way through the tangle and had produced crowns large enough to suppress the thicket.

If the stream-bank vegetation is very thin, and, owing to a scarcity of climber and thicket species, is obviously unsuited to the obstructive method, then the normal partial clearing technique should be used, viz., the occasional thicket and low branching tree would be removed so as to aid the dissipation of the ecoclimate by facilitating the entry of wind.

Should the stream enter a favourable temporary habitat consisting of a closed canopy of forest or woodland, but with no peripheral wind-breaks and no thicket on the stream-banks, partial clearing should also be resorted to. In this case the canopy should be broken by the felling of alternate trees, and any small isolated thickets removed. By letting the light in the forest floor would soon be invaded by grass, which would extend up to the stream-bed and so destroy the temporary habitat's wet season advantage of good visibility, as well as ensuring the annual penetration by fire.

To sum up, where the riverine vegetation is dense, even though narrow, and full of thickets, shrubs and creepers, obstructive clearing should be used, but if it is open then partial clearing should be employed. This combination of obstructive and partial clearing would come under the all-embracing heading of "discriminative clearing," since certain features of the vegetation are being discriminated against.

Obstructive clearing would be unlikely to achieve tsetse eradication if *G. tachinoides* were present, because the removal of the overhead canopy would not affect it (Nash, 1948*a*, p. 33). Whether the blocking of the channel would prevent its finding its hosts is very doubtful, because this species is believed to be able to flit about in quite dense thicket. Nevertheless there are large areas of Nigeria where *G. tachinoides* does not occur, and territories such as Sierra Leone where this species is unknown.

Obstructive clearing would probably succeed where small tsetse-infested streams are found in the forest belt, and where partial clearing would be useless, owing to rapid regeneration. In the secondary evergreen forest belt of Sierra Leone it was noted that where the small streams were completely choked no *G. palpalis* could be found, but that if a flight-line was present this species occurred (Nash, 1948*a*, p. 51).

Even though *G. palpalis* may be found searching for food along thicket-lined creeks and rivers in the complete absence of high shade, nevertheless an overhead canopy is believed to be essential to the formation of a permanent habitat—except possibly near the sea-shore. It is therefore conceivable that even though the stream or river was too wide to be obstructed, the destruction of the overhead canopy alone, over a long stretch of river, might succeed in eradicating *G. palpalis* ; but unless an extensive ruthless barrier clearing was inserted at the uncleared end, the river would certainly become re-infested in the rains.

PART V—THE TRYPANOSOME INFECTION RATE IN *G. PALPALIS.*

During a period of 21 months, 3382 male[6] *G. palpalis* were collected from streams within a 30-mile radius of Katabu ; these were dissected and gave the following infection rates :

Position.	Number infected.	Mature infection rate.	Group.
Salivary glands . . .	1	0·03 per cent.	*Brucei—Gambiense.*
Hypopharynx only . . .	91	3·08 ,,	*Vivax.*
Hypopharynx and gut . .	9	0·30 ,,	*Congolense.*

Total = 101 flies, or 3·3 per cent. for all groups.

The *Vivax* group only will be discussed, as infections with trypanosomes of the other groups are too few.

The monthly infection rates are shown in Table XX ; it is a pity that owing to scarcity of tsetse in this region the rates are not based on larger figures. Some climatic data are also given, as various workers have suggested that the seasonal variations in the infection rate are related to various climatic factors. The rainfall figures are from the Katabu open woodland station, and the temperature data from the composite stream-bed climate at 4 ft. above ground-level ; these are not strictly applicable, as the flies came from many streams in the area.

In each year our infection rates were minimal in December or January—the cold season. Over a period of 12 months Squire (1951) dissected 2313 male *G. palpalis* in the forest belt of Sierra Leone ; he obtained his lowest infection rates for the *Vivax* group around the month of January, when the coldest temperatures of the year occur in the nights and early mornings. We are unaware of any other work on the seasonal infection rate in *G. palpalis*, but Fairbairn (1948) points out how, in the results from dissections carried out on wild *G. morsitans* by Kinghorne, Yorke and Lloyd (1913), no infected flies were found when the temperature ranged between 67·2 and 77·5° F. ; these authors found that the infection rate was greater in the hot than in the cold season, and that in their field laboratory *G. morsitans* failed to transmit *T. rhodesiense* in the cold months, because under such conditions the trypanosome developmental cycle failed to reach completion.

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Returning to Table XX, in 1949 the infection rate rose in the wet season in June and July, remained fairly steady, and then dropped in the early dry season, becoming minimal in December. In 1950 the wet season cycle was much more pronounced, the infection rate rising rapidly from June to become maximal in the height of the rains, August and September, and then crashing down as the rains petered out. If this was the only evidence of a wet season peak, it might be considered inadequate, but Squire (1951) demonstrated a similar peak in September with *G. palpalis* in Sierra Leone, and Lloyd *et al.* (1924), working around Sherifuri in north-eastern Nigeria, showed that the rate for mature infections of *Vivax* reached a peak in July with *G. morsitans*, and in August with *G. tachinoides*.

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[6] Females caught at the same time had to be kept for breeding purposes.

As can be seen from Table XX, the August and September peak of 1950 is not associated with very high temperature, either in those months or in the months immediately previous; hence this peak cannot be explained on the grounds that the effects of high temperature upon the puparia had led to an increased infection rate, as had been found by Burtt (1946*a*) when working on *G. morsitans* and *T. rhodesiense* in the laboratory.

We suggest that, at any rate in the case of *G. palpalis* and *Vivax* in the Kaduna area, the wet season peak is associated with the increase in the average age of the flies during the rains; it will be remembered that this culminated at Katabu in an August fly population made up of 5 different monthly components (see fig. 14B). Such an accumulation of different generations surviving into August signifies the presence of many very old flies in that month, which might be expected to result in a very high infection rate. The drop in the infection rate in October may be associated with the great decrease in the size of the fly population in that month (see fig. 14A), signifying the death of many of the old flies.

The above explanation is believed to be equally applicable to *G. morsitans* and *G. tachinoides*. Lloyd *et al.* (1924) arrived at the same explanation for their wet season peak, but accidentally, because their assumptions were wrong. They argued that because they could not find puparia in the rains, breeding had stopped, and that therefore there could be no young flies; hence, owing to the absence of young flies, *the average age of the wet season fly population must be greater*. Although their conclusion was right, it was based on a false premise, because Nash (1939), working in the *same* area, demonstrated that puparia of both species could be found throughout the rains. Earlier, Nash (1936) had shown, as described on p. 139, that the longevity of both *G. morsitans* and *G. tachinoides* increases, and remains high throughout the rains, when the oldest individuals (amongst marked flies) are found.

Squire (1951) did not accept the conclusion given by Lloyd *et al.* (1924), because he found a peak emergence of young *G. palpalis* at the time when he got his peak infection rate in the rains; he therefore argued that since there were many young flies, there must be a great dilution in age, and that therefore there was no reason to suppose that the average age of the flies was greater in the rains, and that therefore the conclusion of these workers must be wrong and another explanation sought. Unfortunately Squire's method of age-grouping does not indicate the seasons at which the average age of the fly population is greatest, but we believe that it is quite likely that the explanation of his September peak infection rate *is* a greater average age of the flies, due to increased longevity in the first part of the wet season.

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TABLE XX.—*The percentage of male* G. palpalis, *from various localities around Katabu, which showed mature infections of the* Vivax *group ; also relevant climatic data.*

	1949.								1950.												1951
Month :—	V.	VI.	VII.	VIII.	IX.	X.	XI.	XII.	I.	II.	III.	IV.	V.	VI.	VII.	VIII.	IX.	X.	XI.	XII.	I.
Total males dissected	180	113	216	398	275	199	176	219	140	115	86	87	126	102	216	192	154	90	179	69	50
Mature *Vivax* group, per cent.	1·7	2·7	3·2	2·8	3·3	3·0	2·8	0·5	2·9	6·0	5·8	2·3	0·0	1·0	2·3	5·2	5·2	1·1	1·7	0·0	0·0
Rainfall (inches)	5·9	8·7	5·8	14·0	4·7	1·5	0·0	0·0	0·0	0·0	0·0	3·5	4·1	6·3	3·9	13·7	5·9	3·9	0·0	0·0	0·0
Mean temp. (° F.)	77·9	75·2	73·4	72·5	74·0	73·9	68·8	66·3	68·5	70·4	74·7	78·5	77·1	75·6	72·9	70·9	72·8	72·8	70·3	69·0	70·6
Mean max. temp. (° F.)	82·5	80·5	77·4	76·3	78·5	80·8	79·9	78·8	79·6	81·7	87·7	88·7	81·5	81·4	76·5	73·4	77·1	80·8	82·4	82·1	83·2
Mean min. temp. (° F.)	73·4	69·9	69·4	68·7	69·4	66·9	57·7	53·7	57·3	59·0	61·7	68·3	72·7	69·8	69·4	68·4	68·4	64·8	58·2	55·9	58·0

Returning to Table XX, it will be seen that the infection rate for *G. palpalis* rises from its low level in the cold month of December, 1949, to reach a peak in the latter part of the dry season, February and March, 1950, and then drops to nothing in May of the early rains. Unfortunately, there are only data for this part of the cycle for one year. Squire (1951) shows a very similar cycle in his infection rates for male *G. palpalis*, the figures rising from 0·0 in January, to 5·5 in April, and dropping to 3·8 in June ; his cycle is a month later than ours ; whereas our peak period occurs in the last two months of the dry season, his occurs in the first month of the rains. There appears to be no correlation between our peak period and high temperature. It should be remembered that even if further work confirms the existence of a February and March peak, its practical importance would be reduced in northern Nigeria by the relatively low expectation of life of males, especially in February (see Table XI and fig. 9).

Our minimal infection rate in May, 1950, when fly density is lowest, may be due to the youthfulness of the tsetse population—most of the old flies having been killed off by the high maximum temperatures of March and, in this year, of April also because the rains were late, see p. 127.

Lloyd *et al.* (1924) show no strictly comparable dry season cycle for *G. morsitans* and *G. tachinoides*. It would be wiser therefore to ignore this part of the annual cycle until there is more evidence available.

* * * * *

Burtt (1946*a*), and subsequently Fairbairn and Culwick (1950), showed conclusively that with *G. morsitans* high temperature is of the greatest importance in enabling *T. rhodesiense* to develop and invade the salivary glands, and hence in bringing about a great increase in the ability of the flies to become infected and to transmit sleeping sickness. It is therefore likely that *T. gambiense*, which also invades the salivary glands, is similarly affected by high temperature, and that therefore *G. palpalis* is likely to be more dangerous to man in the hot weather. But our infection rates, quoted above, suggest that in the case of the *Vivax* group, which becomes mature in the hypopharynx, there is no definite relationship in the field between high temperature and a high infection rate, and that therefore there is no reason to think that the danger to cattle is greatest in the hot weather.

Clearly there is need for much more work on this subject both in the laboratory and in the field ; it is suggested that in the field continuous records are needed for 3 or 4 years if the cycle is to be properly elucidated.

Conclusions.

1. Out of 3382 male *G. palpalis* collected over 21 months from streams in the Kaduna-Katabu area, 3·3 per cent. showed mature infections.

2. It was found that mature infections of the *Vivax* group were 10 times more frequent than those of the *Congolense* group, and 90 times more frequent than those of the *Brucei-Gambiense* group. The following conclusions refer to mature infections of the *Vivax* group only.

3. The highest infection rates in the field do not appear to be associated with the hottest weather.

4. *a.* The lowest infection rates in the field appear to be associated both in

Nigeria and in Sierra Leone with the period in the dry season when relatively very low temperatures are recorded near dawn.

b. It would seem therefore that in the cold, dry season little infection can take place amongst cattle grazed in *G. palpalis* areas.

5. After the rains have become established the infection rate increases greatly, to reach a peak around August or September; this occurs in both Nigeria and Sierra Leone. A similar peak infection rate occurs in both *G. morsitans* and *G. tachinoides* in the height of the rains.

6. It is suggested that the wet season increase in the infection rate found in *G. palpalis*, *G. tachinoides* and *G. morsitans* is associated with increased longevity in the early rains, which produces a fly community whose average age is maximal when the peak infection rates are recorded.

7. The nomadic Fulani of Nigeria migrate in the early dry season, southwards, into the fly areas in search of grazing, but they always return to the extreme fly-free north in the early rains. Possibly past experience has taught them that it is fatal to their cattle to spend the heavy rains in fly areas, when all three species of tsetse are heavily infected with trypanosomes.

PART VI—SUMMARY.

1. Over a period of six years, a population of *G. palpalis* was studied in great detail along 2400 yards of stream, situated near the northern limit of the range of this species in Nigeria.

2. The methods used included regular fly-rounds along which all tsetse caught were marked and liberated, regular puparia-rounds, and the keeping of fly populations in tubes in different parts of the stream-bed.

3. Two meteorological stations were set up in the fringing forest and one in the adjacent woodland savannah. There is a definite ecoclimate within the forest which is far more equable than the general climate of the woodland, p. 82 and fig. 2.

4. Of the two forest stations one was sited in a reach where the stream always dries up, and the other beside permanent pools. In the wet season there is no appreciable difference in the two ecoclimates, but in the late dry season conditions are far less severe near the pools around which the tsetse concentrate. See p. 131, Table XIV, February and March.

5. In the two forest stations measurements were made at both 4 ft. and 4 in. above ground-level. In the rains the ecoclimate is almost the same at both heights (p. 83, Table II), as it is in the dry season in the waterless stream-bed (p. 131, Table XIV). In the late dry season of *mild* years, even by the pools, the climatic differences at the two heights are not very great (Table II), but in *severe* years it becomes apparent that there is a very pronounced microclimate at 4 in. above wet sand, the climate being much less severe than at 4 ft. (pp. 85–86, Table III).

6. This microclimate provides protection against extremes of high temperature, and *prolonged* exposure to very low humidity: during six years of observations the temperature never rose above 90° F. (32·2° C.) or fell below 49° F (9·4° C.); the humid air of the microclimate may be temporarily dissipated by wind, in which case for a short time the relative humidity may fall as low as 23 per cent. at 89° F. (pp. 85–86, and Table III).

7. In the microclimate, conditions remain remarkably constant from year to year, p. 87, although considerable *annual* variation in the severity of the late dry season may be recorded in the woodland and forest ecoclimate at 4 ft. (pp. 88–90 and fig. 3).

8. It has been found that in the dry season *G. palpalis* tends to concentrate in the vicinity of the microclimate, which, even in the most severe years, ensures the survival of a few tsetse (pp. 91–93).

9. The amount of water found in a stream and therefore the *extensiveness* of the microclimate varies from year to year, being largely dependent upon the height of the water table and therefore upon the rainfall of the preceding year or years (pp. 90–91 and Table IV), as well as upon the severity of the current dry season (fig. 3).

10. The degree of concentration is far greater in severe years when the microclimate is most restricted (pp. 95–98.)

11. *a*. In years when concentration is maximal, *G. palpalis* is restricted to the vicinity of certain pools which never dry up. African villages are sited near such pools; it therefore follows that, in severe years, following upon abnormally low rainfall, a very close, personal man-fly contact is established, which is liable to lead to an increased transmission of human sleeping sickness (p. 98); the high temperature of this season may further facilitate transmission (p. 79).

b. In such years it is suggested that at the start of the dispersal season the disease may be introduced to adjacent villages by infected flies moving up- and down-stream (p. 98).

12. *a*. In years when concentration is minimal, water being abundant and *G. palpalis* ubiquitous along the streams, there is likely to be little transmission of human trypanosomiasis owing to the impersonal nature of the man-fly contact at the water holes, which will also be less used by man owing to a better water supply from the village wells (p. 98).

b. However, one would expect a higher infection rate amongst the nomadic cattle which graze the new grass along miles of stream-bank, which in such years will be continuously infested by tsetse (pp. 98–99).

13. *a*. The season of long travel by *G. palpalis* starts at the beginning of the heavy rains (becoming greatest at the end of this period) and lasts for 9 months, ending when the weather becomes very hot (p. 94 and Table V).

b. The period when travel is minimal covers the last month of the dry season, and the first two months of the rains; it is suggested that the bulk of human trypanosomiasis is transmitted in these 3 months of the year (p. 94).

14. *a*. The two sexes indulge equally in long travel (p. 95).

b. Within 24 hours flies frequently travel 1000 yds., and 2000 yds. is not uncommon. One fly covered just under 2 miles in a day.

c. The longest distance a marked fly travelled along the stream was just over 3 miles (5 km.).

d. Two marked flies are known to have crossed one mile of woodland to reach another stream system.

* * * * *

The following conclusions are based on a study of the longevity of *G. palpalis*, kept in tubes in the stream-bed during the critical latter half of the dry season of a severe year (pp. 122–133).

15. *a*. The reason why wild flies evacuate the waterless reaches of a stream at this season is because failure to do so would result in their virtual extermination, brought about by increases in the maximum temperature and maximum saturation deficit.

b. Over ten-day periods, average maximum temperatures of 88° F. (31° C.) are associated with an abnormally high mortality among a population composed of both sexes (p. 129); however, the males are seriously affected by average maximum temperatures of only 84° F. (28·9° C.), the females not being equally affected until 91° F. (32·8° C.); extermination of the population occurs when such temperatures reach 93–95° F. (34–35° C.) (p. 132).

c. This suggests that the partial clearing of riverine vegetation should be effective in places where the meteorological station records show that the maximum shade temperature may average 95° F. (35° C.) over a ten-day period; possibly an average of 91° F. (32·8° C.) over two consecutive months might suffice.

d. Flies which spend their early life in a severe climate can tolerate higher maximum saturation deficits than those accustomed to a milder climate (p. 129).

e. Females, being more tolerant than males to high temperature and saturation deficit, should be more numerous in the wild fly population which survives the late dry season (p. 132).

f. Flies from 10–50 days old seem to be less susceptible to severe climatic conditions than flies from 0–10 or 50–90 days old. This suggests that the fly population which survives the late dry season should be composed of rather young individuals (p. 125).

g. Conditions at this season become sufficiently severe to cause abnormal mortality—even in the microclimate (p. 127 and Table XIV). This suggests that the fly population which survives the late dry season should be greatly reduced in numbers.

* * * * *

The following conclusions on the expectation of life of *wild G. palpalis* are based on the recapture of marked flies. Our figures for life expectation are conservative estimates (pp. 114–120).

16. *a*. At the extreme end of the rains the expectation of life of both sexes is temporarily high. It then falls rapidly, to become minimal in the mid-dry season, because the attainment of old age will be rendered impossible by the approaching rigours of the late dry season which discriminate against the older flies. At the start of the rains the expectation of life is greatest, because the surviving population is young and has some months of very favourable conditions ahead. As the rains become heavier expectation decreases slightly but steadily; this trend is abruptly reversed as soon as the rains start to abate (pp. 115–117).

b. The maximal expectation of life at the start of the rains is likely to be a very important factor in the spread of human trypanosomiasis, see Nos. 11. *a*. and 13. *b*. above; it may also be important for the spread of bovine trypanosomiasis, as the Fulani trek their cattle north at this season (p. 117).

c. The temporarily high expectation at the end of the rains is unlikely to be of medical importance because the village wells are full, and man-fly contact at the water holes is impersonal; however, it may be of veterinary importance because the Fulani make their southward trek in the early dry season (p. 117).

d. The minimal expectation of life among the flies found in the cold mid-dry season, suggests that there should be relatively little danger to man or animals from these flies (p. 118).

17. *a*. Our conservative estimate for the average age of wild females ranges, according to the season, from 6 to 15 weeks, and for wild males from 4 to nearly 8 weeks (p. 115, Table X).

b. Whereas the percentage of recaptured females of an age *known* to exceed 2 calendar months may exceed 50 per cent., with males the figure never exceeds 7 per cent. (p. 119, and Table XI).

c. During four years the total number of females with over 4 calendar months of *known* life composed 1·2 per cent. of the total recaptures; for males the figure was 0·3 per cent. (p. 119).

* * * * *

As the above estimates are of a conservative nature, in order to obtain an insight into the *potential* longevity of *G. palpalis* flies were kept during the dry seasons of two mild years in tubes in the stream-bed by the permanent pools; conditions were believed to be nearly ideal (pp. 120–123). The following results were obtained:

18. *a*. About one-quarter of the flies of each sex die within 20 days of birth (p. 122).

b. Females: After the high initial "infantile" mortality there follows a period—21 to 60 days—in which very few deaths occur; about half the females die between the 61st and 140th day; the remaining one-fifth die between the 141st and 233rd day (p. 122).

c. Males: After a high "infantile" mortality there follows a period of fewer deaths, but nevertheless half the males die between the 21st and 80th day; the remaining quarter die between the 81st and 168th day (p. 123).

d. Three-quarters of the male population are dead by the 80th day, as against the 130th day for females (p. 123).

19. Tubed flies kept in the stream-bed during the rains gave results of little value. Confinement would appear to intensify greatly the factor, associated with an almost saturated atmosphere, which reduces the expectation of life of wild flies in the heavy rains (see No. 16*a* above, and p. 121).

20. Under tubed conditions, during the rains both sexes live longer at 4 ft. than 4 in. above ground-level; during the dry season males live longer at the lower level, whereas the females live equally well at either height until the very hot weather, when they also do better at the lower level (pp. 121 and 133).

* * * * *

21. With regard to the *extremes* of age attainable by *G. palpalis*, at favourable seasons females can definitely live up to 6 calendar months in nature, but in captivity they can attain almost 8 months; males can certainly live almost 5 months in nature but in captivity they can achieve 5½ months. However, only a very small proportion of the population is likely to achieve such extreme age (p. 123).

22. On the ground of greater longevity, as shown for both wild and captive flies, the female sex should be the more dangerous vector of trypanosomiasis (p. 120 and p. 122).

* * * * *

23. Despite the impression given by the results from puparia-searching that breeding is virtually confined to the dry season (p. 103), it really continues throughout the year. Pregnancy dissections show that at the drier end of the range of *G. palpalis* there is no wet season cessation of breeding (pp. 107–108 and Table VIII).

24. Reasons are given for supposing that under certain conditions a high pregnancy rate may indicate a low reproduction rate, and *vice versa* (pp.108–109).

25. From observations in the laboratory the rate of reproduction in the field is believed to be greatly reduced by the low temperatures of much of the dry season ; the rate increases greatly with the high temperatures of the late dry season and early rains (pp. 110–111).

26. The temperature of the pupal environment has been recorded for three years. The average monthly temperature at ½ in. depth ranged from 65°–76° F. (18·3°–24·4° C.) ; the mean monthly maximum temperature never exceeded 86·6° F. (30·3° C.), and the mean minimum never fell below 57° F. (13·9° C.). Records were also kept for 1½ in. depth, and showed that the mean temperature was never more than 2° F. lower at this greater depth (pp. 111–113 and Table IX).

27. *a.* In the heavy rains *G. palpalis* does not appear to larviposit far out in the open woodland, but in many scattered sites along the higher ground near the junction of the fringing forest and savannah ; here the puparia are safe from inundation except in years of quite exceptionally heavy rainfall (pp. 105–107).

b. In such years the forest near the source of a stream, owing to the smaller catchment area, may prove to be a valuable survival focus when inundation of the breeding-grounds further down-stream has led to a great destruction of puparia (pp. 105–107).

28. The annual cycle of seasonal fluctuations in fly density is as follows : From a peak density in the heavy rains, the fly population decreases rapidly as the rains peter out, and then gradually throughout the dry season, to become minimal at the beginning of the following wet season ; this reduction period extends from October until April or May. There then follows a recovery period in the early rains in which the fly population starts to increase slowly, and then very rapidly, to reach a peak in the heavy rains ; this recovery period extends from May until August or September (pp. 99–102).

29. The Reduction Period : The rapid decrease in the fly population at the end of the heavy rains is due to reduced longevity associated with the recent occurrence of very low saturation deficits, combined with a diminished breeding rate associated with lower mean temperatures (p. 99 and p. 138).

The gradual decrease throughout the dry season is due to a general reduction in longevity associated with an unfavourably high saturation deficit, and to a great decrease in the breeding rate associated with the cold dry season ; in the late dry season longevity is further reduced by dangerously high maximum temperatures leading to a minimal tsetse population (pp. 137–138).

30. The Recovery Period : The great increase in the tsetse population in the first part of the rains is due to exceptionally long life, associated with inter-

mediate saturation deficits and the absence of lethal maximum temperatures, combined with a greatly increased breeding rate associated with very high mean temperatures (p. 138).

31. Longevity is reduced at high and very low saturation deficits, but increased at intermediate saturation deficits. Mean monthly saturation deficits above 9 mb. (7 mm.) or below 2 mb. (1·5 mm.) are associated with a decrease in the tsetse population (p. 137 and p. 139).

32. The breeding rate increases with rising temperature. Mean monthly temperatures above 73° F. (22·8° C.) are associated with an increase in the tsetse population two months later, whereas mean temperatures below 73° F. are associated with a subsequent decrease (p. 137 and p. 109).

33. A study of climatic conditions in the early rains, when all factors combine to promote a great increase in the population of *G. palpalis*, suggests that optimal laboratory conditions are provided by a constant temperature of 77° F. (25° C.) with a relative humidity of 83 per cent. (S.D. = 5·3 mb.). Such conditions have proved satisfactory for the large-scale breeding of this tsetse in the laboratory (p. 84).

34. The results quoted hitherto, strengthened by observations on the effects of a natural disaster to the fly population described on pp. 101–102, suggest that on ecological grounds the following timing should be adopted for control measures directed against *G. palpalis*:—Operations should be started when the rains are due, and the fly population minimal; they should be continued throughout the recovery season, after which the extermination of any survivors can be left to the natural factors associated with the ensuing reduction period. There will be no chance for fly numbers to increase until the following rains, by which time eradication should have been achieved (p. 103). (*N.B.*—This would entail the reversal of the hitherto accepted procedure of applying control measures in the dry season).

35. *a.* Out of 17,306 *G. palpalis* caught at Katabu over six years, 49 per cent. were females; out of 3892 flies caught ten miles away on the control fly-round, 46 per cent. were females; among 1903 flies bred from wild puparia, 52 per cent. were females. There is thus no evidence that in this area females are reluctant to appear to man, or that they are appreciably less active than males; this agrees with previous findings from northern Nigeria (pp. 102–103).

b. However, at Katabu there was a definite tendency for the percentage of females caught to be rather higher in the dry weather than in the wet. In every year there was a sharp drop in this percentage when the evaporation rate fell in the early rains (p. 102).

* * * * *

36. Out of 3382 male *G. palpalis* collected over twenty-one months from streams in the Kaduna-Katabu area, 3·3 per cent. showed mature trypanosome infections. As 3·1 per cent. of the flies were infected with trypanosomes of the *Vivax* group, only results for this group are given below (p. 157.)

37. The lowest infection rates occur in the cold dry season, which should therefore be the safest season for cattle in *palpalis* areas (p. 157 and p. 161).

38. The highest infection rates do not appear to be associated with the hottest weather (p. 160).

39. After the rains have become established the infection rate in *G. palpalis* increases to reach a peak in the heavy rains. Peaks have also been recorded

at this season for *G. morsitans* and *G. tachinoides* in northern Nigeria. It should be noted that, for each of these three species of tsetse, the high wet season infection rate tends to coincide with the period when the oldest flies are found (pp. 157–158).

40. Since all three species are liable to be very heavily infected with trypanosomes in the heavy rains, it is not surprising that in the early rains the nomadic Fulani drive their cattle from the tsetse areas to the fly-free north.

* * * * *

41. *G. palpalis* can thrive on a diet of virtually only baboon, duiker, Monitor lizard and possibly monkey blood ; the blood of the medium and larger species of game is unnecessary (pp. 140–143).

42. The fly experiences definite hunger at the height of the heavy rains when the fringing forest is inundated ; this may be a contributory factor to the reduction in the size of the tsetse population at this season (p. 142).

43. The following features are essential to the formation of a permanent habitat :—The presence of good lateral and vertical insulation provided by evergreen vegetation, and a free flight-line along the stream-bed or through the forest to permit travel from dense shelter to the feeding grounds. If the fringing forest is narrow, the presence of permanent pools of water will be seasonally essential, but the stream banks must be steep and sharply defined so as to aid the vegetation in preventing the dissipation of the microclimate by wind (pp. 149–151 and p. 154) ; however, these latter features are unneceassry if the fringing forest is extensive and well-insulated (pp. 147–148 and p. 153).

44. *a*. Favourable temporary habitats play a great part in the recovery period, enabling the fly population to re-establish a high density before the ensuing reduction period.

b. The following are common characteristics of the structure of such a habitat :—Lateral insulation is usually absent, but there is continuous vertical insulation leading to suppressed undergrowth and good visibility, and thus providing extensive feeding-grounds during the long grass season. Small thickets are present, affording temporary breeding sites until the weather becomes too severe. The vegetation is usually of a mixed-deciduous type (p. 154).

45. *a*. Our vegetation studies suggest the possibility of a new clearing technique against *G. palpalis*, for use where the fringing forest is demarcated by a wall of shrubs and climbers, and is roofed over by a canopy composed of the creeper-covered crowns of medium-sized trees. It is proposed that the trees of the canopy should be felled so as to block the stream, but that the shrubs, thickets, creepers and any giant emergents should be spared. This would result in a stream-bed lacking in vertical insulation, and choked by low thicket which should prevent travel by the fly within its ecoclimate. Such a method might be referred to as " obstructive clearing " (pp. 155-157).

b. Obstructive clearing should be of value in the savannah belt wherever climber and thicket species are common components of the fringing forest ; if successful, it would reduce the initial clearing costs, and eliminate the need for maintenance. In the forest belt it might prove invaluable under conditions where normal clearing methods could not be contemplated, owing to the rapid rate of regeneration.

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APPENDIX I.

The Ecoclimate Experienced by *G. palpalis* at Katabu and by *G. tachinoides* at Gadau, both places near the Northern Limit of Each Species' Respective Range.

(Means over 3 years at Katabu, 1947–1949, and over 2 years at Gadau, 1934–1936 ; records from 4 feet above ground-level.)

Month.	Rainfall (inches).		Maximum temp. (° F.).		Minimum temp. (° F.).		Temperature range (° F.).		Mean temp. (° F.).		Relative humidity % at mean temp.		Mean evaporation (c.c.).		Mean saturation deficit (mb.).	
	Katabu.	Gadau.	Katabu.	Gadau.	Katabu.	Gadau.	Katabu.	Gadau.	Katabu.	Gadau.	Katabu.	Gadau.	Katabu.	Gadau.	Katabu.	Gadau.
Nov.	0·0	0·0	79·5	88·0	58·0	58·5	21·5	29·5	69·0	73·5	69	60	13·0	28·0	7·4	11·2
Dec.	0·0	0·0	79·5	83·0	55·5	55·5	24·0	27·5	67·5	69·5	54	54	24·0	29·0	10·4	11·5
Jan.	0·0	0·0	80·5	83·0	57·5	55·0	23·0	28·0	69·0	69·0	49	45	25·0	32·5	12·3	13·2
Feb.	0·0	0·0	82·5	90·5	59·5	59·5	23·0	31·0	71·0	75·0	43	37	28·0	42·5	14·5	18·4
Mar.	0·5	0·0	86·0	98·5	66·5	67·5	19·5	31·0	76·0	84·0	50	36	27·0	51·5	15·3	25·0
Apr.	3·0	2·7	84·5	97·0	72·5	72·0	12·0	25·0	78·5	84·5	74	46	13·0	47·5	8·5	22·1
May	5·0	2·0	81·5	97·0	72·5	76·5	9·0	20·5	77·0	87·0	85	62	7·0	30·5	4·8	16·4
June	8·2	3·4	79·5	89·0	69·5	74·0	10·0	15·0	74·5	81·5	89	75	5·0	19·5	3·1	9·3
July	8·2	5·8	77·0	84·0	69·5	73·5	7·5	10·5	73·5	79·0	89	82	5·0	12·0	3·0	6·1
Aug.	12·6	11·2	76·0	79·5	69·0	71·5	7·0	8·0	72·5	75·5	94	91	4·0	4·5	1·7	2·7
Sept.	8·5	4·7	78·0	81·0	68·5	72·5	9·5	8·5	73·5	77·0	91	92	4·0	5·5	2·6	2·4
Oct.	0·9	0·2	80·0	87·0	65·0	70·5	15·0	16·5	72·5	79·0	82	78	11·0	17·0	4·9	7·2

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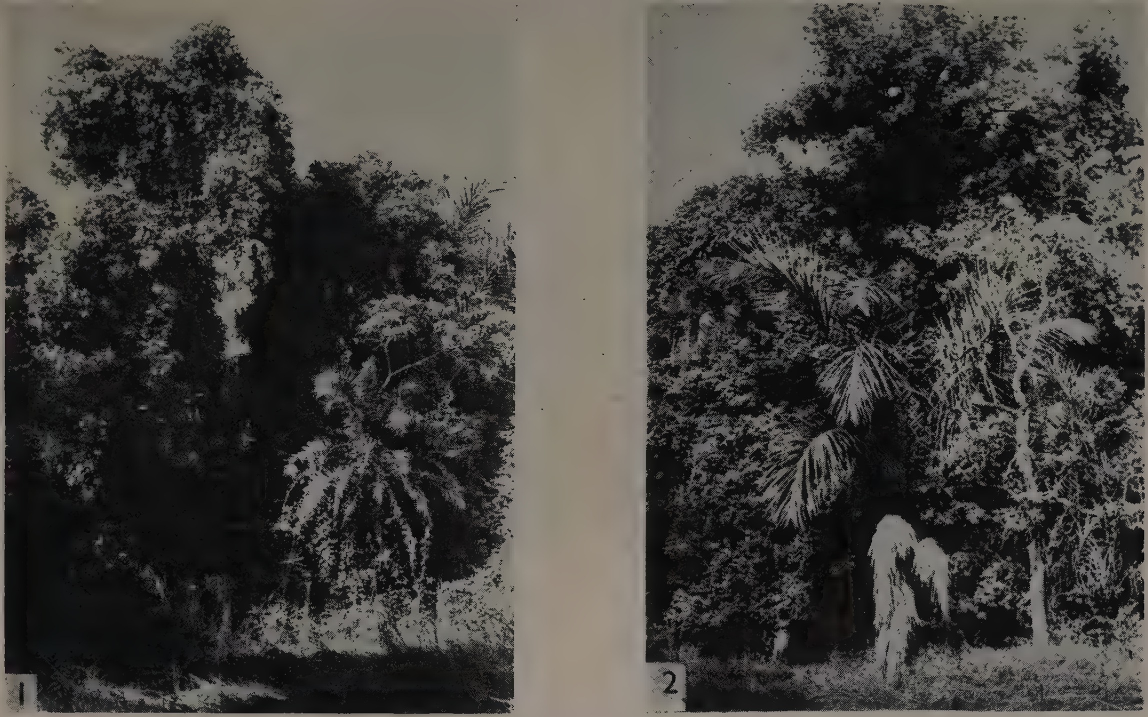
PLATE I.

THE LATERAL VEGETATIONAL INSULATION OF A PERMANENT HABITAT.

FIG. 1.—A fire- and wind-resistant vertical creeper curtain of evergreens preserves the ecoclimate. (*N.B.*—Phoenix palm on right, and Raphia palm protruding out of canopy, top right.)

FIG. 2.—A fire- and wind-resistant wall of evergreen shrubs and Raphia palm preserves the ecoclimate within the forest.

PLATE I.



The lateral vegetational insulation of a permanent habitat.

T. A. M. Nash and W. A. Page.

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PLATE II.

POTENTIAL FEEDING GROUNDS WITHIN THE ECOCLIMATE OF A MAJOR PERMANENT HABITAT.

FIG. 1.—A very heavy, low canopy completely suppresses the undergrowth, providing a potential feeding-ground when the climate is very severe outside. This is also an important breeding-ground.

FIG. 2.—A high canopy partially suppresses the undergrowth and provides a potential feeding-ground within the forest.

1

2

Potential feeding-grounds within the ecoclimate of a major permanent habitat.

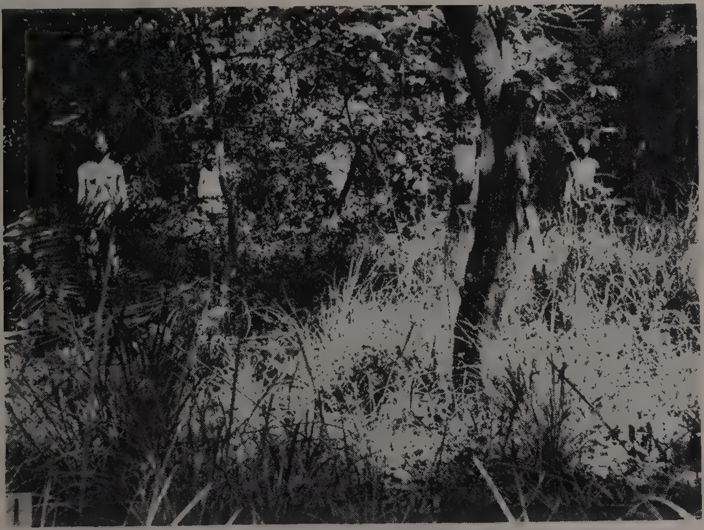
T. A. M. Nash and W. A. Page. *Adlard & Son, Ltd., Dorking.*

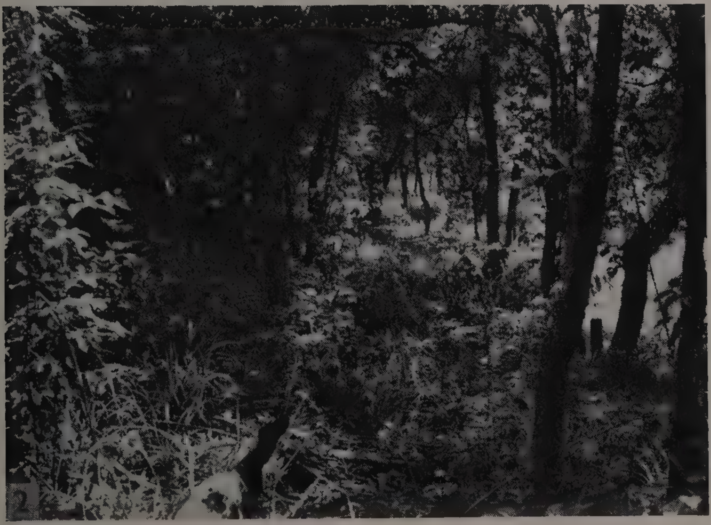
PLATE III.

POTENTIAL FEEDING-GROUNDS ON THE EDGE OF A PERMANENT HABITAT.

FIG. 1.—Without leaving the habitat, the tsetse can inspect the bay of intrusive savannah for hosts.

FIG. 2.—The forest habitat (left) may be bordered (right) by close-growing woodland whose canopy partially suppresses the grass, producing an excellent feeding-ground which the fly can explore when the weather is mild.





Potential feeding-grounds on the edge of a permanent habitat.

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PLATE IV.

A MINOR PERMANENT HABITAT, AND ITS FEEDING-GROUND.

FIG. 1.—A permanent pool. Note the steep, high banks which retain the microclimate, despite rather poor vegetational insulation. Note the clear flight line. The man is looking towards the ford, see fig. 2 below. Red Section, 4–5.

FIG. 2.—The ford is open, but well-shaded by a high canopy. The savannah is behind the man. Red Section, 4–5.

A minor permanent habitat, and its feeding-ground.

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PLATE V.

A Very Favourable Temporary Habitat.

Fig. 1.—Suppressed undergrowth under overhead canopy produces excellent feeding-grounds, especially in the long grass season. The twisted mass of huge liana stems on the ground is a much favoured breeding site.

Fig. 2.—If the temporary habitat is to be favourable there should also be small thickets, as shown on left. Such thickets act as breeding-grounds and provide adequate shelter in the early dry season.

A very favourable temporary habitat.

T. A. M. Nash and W. A. Page.

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PLATE VI.

UNFAVOURABLE TEMPORARY HABITATS.

FIG. 1.—View right across fringing forest, which consists of a low understorey beneath a high shade canopy. (*N.B.*—There are no small thickets and no peripheral curtain.) White Section 10–11.

FIG. 2.—Dense, secondary thicket of mixed deciduous species, with no overhead canopy. Blue Section.

Unfavourable temporary habitats.

PLATE VII.

A Very Unfavourable Temporary Habitat.

Fig. 1.—Very narrow fringing forest which can be seen through. (*N.B.*—Man on far bank with grass behind him.) Red Section, 1–2.

Fig. 2.—The stream-bed is shallow as shown by the man. The vegetation grows out of the stream-bed frequently blocking the flight-line. Most unfavourable, despite permanent pools. Red Section, 1–2.

PLATE VII.

A very unfavourable temporary habitat.

T. A. M. Nash and W. A. Page.

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ON THE NUTRITION OF *CARPOPHILUS HEMIPTERUS* L. (COLEOPTERA: NITIDULIDAE).

By G. O. Stride, Ph.D., F.R.E.S.

(*Department of Zoology, University of Bristol*).[1]

Manuscript received 15th October, 1952.

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With 11 Text-figures.

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1. Introduction.

The factors which govern the survival of a species of insect on various foods are of considerable interest. They may also be of economic importance when the insect concerned feeds on some product of economic value. Certain insects have been shown to possess dietary requirements which limit them to particular foods. *Dermestes maculatus* (Degeer) (Gay, 1938) appears to be restricted to foods of animal origin, since these alone contain the sterols it requires. When reared on artificial diets, *Ephestia kühniella* Zeller appears to require less riboflavin than *Ephestia cautella* Walker or *Ephestia elutella* Hübner.

---

[1] Now at University College of the Gold Coast, Achimota, Gold Coast.

Patent flours contain very little riboflavin, and it has been suggested that this insensitivity to a lack of riboflavin enables *Ephestia kühniella* to infest flour mills. These mills are not normally infested by the other two species (Fraenkel and Blewett, 1946).

It is known that micro-organisms can play an important role in the nutrition of insects. These micro-organisms may be divided into two biological classes:

i. Species normally present in the external environment.

ii. Species that are intracellular or gut symbionts adapted for a symbiotic existence with insects.

Micro-organisms may increase the supply of growth factors available to the insect. They may thus enable insects to utilise a wider range of foodstuffs than would otherwise be possible. As a pest of stored products *Carpophilus hemipterus* is mainly noted for its attacks on dried fruit, but it also occurs on farinaceous material of a rather different character (Hinton, 1945 : 91).

The present investigation was undertaken to determine why *C. hemipterus* was able to attack such a wide range of products and also to investigate the importance of micro-organisms in its nutrition. In the absence of living micro-organisms the beetle larvae were found to be entirely dependent on the food for supplies of at least four essential vitamins. This suggests that internal symbionts, even if present, do not play an important role in nutrition. The larvae were unable to survive in the absence of living micro-organisms unless substantial quantities of dried yeast were added to the foodstuff. It appeared that dried fruit served as a medium on which micro-organisms could grow. The presence of these micro-organisms converted the dried fruit into a favourable food for the larvae.

Carpophilus hemipterus larvae can only develop rapidly if the diet has a relatively high water content. Any increase in the moisture content of dried fruit would probably encourage infestation by *C. hemipterus* both directly, through the beneficial effect on the larvae, and indirectly, by stimulating the development of micro-organisms.

Since micro-organisms will thrive in almost any moist organic material, one has still to account for dried fruit being more frequently attacked than other stored products. Observations made during the development of a suitable sterile technique may be significant. During this experimental work many food tubes became contaminated, as a result of faulty techniques, by apparently pure cultures of various fungi and bacteria. In general, larval growth was only stimulated when the invading organisms were fungi. Bacteria did not apparently contain the necessary nutrients. Dried fruit contains a higher proportion of sugars than do most stored products. It thus tends to favour the development of yeasts and other fungi. This, in turn, may render it more susceptible to attack by the beetle.

II. METHODS.

a. *Culturing.*

A culture of *Carpophilus hemipterus* was kindly provided by the pest Infestation Laboratory, D.S.I.R., Slough. The culture methods used were based on those in use at the Pest Infestation Laboratory. At first beetles were cultured in breffits containing boiled dates. The dates were boiled for about ten minutes and then drained and cooled. Two or three " layers " were placed in the bottom of each breffit and about a tablespoonful of dried yeast (Glaxo, debittered) was sprinkled over them. The cultures were kept in a constant temperature of 25° C. and a constant relative humidity of 75 per cent.

In the preliminary work eggs were obtained by confining the adult beetles in clean glass dishes with damp folded filter-paper. The beetles laid eggs freely in the folds of the filter paper. Unfortunately it was necessary to disturb the dates in the stock cultures in order to obtain the adults. This affected the stock cultures adversely.

For the later part of the work a more convenient method of culturing the beetles and obtaining the eggs was adopted. It had been noticed that the beetles tended to lay eggs through the gauze covering the mouth of the breffits. If glass slides were placed lightly on the gauze, many eggs were laid between the slides and the gauze. This method was used to obtain eggs without disturbing the cultures. Finally, the beetles were cultured in small three-ounce bottles. Normally, the bottles were closed with corks in which were holes covered with gauze. When eggs were required, the cork was replaced by a square of organdie material, which was held in place by screwing on a bakelite cap. Under these conditions the beetles laid many eggs between the organdie and the bakelite cap. The beetles appear to lay more readily in clean surroundings, and few eggs were laid if the organdie became dirty.

Before pupation the larvae passed through a wandering non-feeding stage, when they crawled over the surface of the food. At this time it was easy to empty them into clean glass dishes, where they would eventually pupate. At a temperature of 25° C. and a relative humidity of 70 per cent. the adults emerged within a week of pupation. The pupae dry up if the relative humidity is allowed to fall too low.

A further advantage was gained by culturing the beetles in many small bottles rather than a few large breffits. Any bottle could be completely discarded if mites appeared in it without seriously impairing the strength of the cultures. Mites were extremely difficult to control in the larger cultures, although all the normal precautions were taken, such as oil baths and autoclaving the food and apparatus.

In order to ease the work involved in the routine culturing of the beetles, about six dozen of the small bottles were supplied with dates and yeast at a time. The bottles were plugged with cotton-wool and the bakelite caps screwed on. They were sterilised by autoclaving. The bottles then remained in good condition for many weeks. A supply of culture bottles sufficient for several weeks could thus be prepared at one time.

b. *The Composition of Artificial Foods.*

The chemical composition of various stored products known to be attacked by *Carpophilus hemipterus* was obtained from McCance and Widdowson (1946). These figures are quoted in Table I. Consideration of the figures in Table I suggested that fatty substances were likely to be of little importance in the nutrition of *C. hemipterus*. It also appeared probable that the beetle would tolerate a fairly wide range of carbohydrate/protein ratios. Although it occurs on cereals, its heaviest infestations are usually on dried fruit.

In a series of preliminary experiments the larvae were reared on mixtures

TABLE I.

Food.	Water.	Fat.	Available carbohydrate.	Protein.
Rice	11·7	1·0	86·8	6·2
Peanuts	4·5	49·0	8·6	28·1
Sugar	·	·	100·0	·
Preserved figs . . .	16·8	Trace	52·9	3·6
Dried apricots . . .	14·7	,,	43·4	4·8
Dried prunes . . .	23·3	,,	33·5	2·0
Fresh plums . . .	84·1	,,	9·6	0·6
Raisins	21·5	,,	64·4	1·1
Sultanas	18·3	,,	64·7	1·7
Fresh peaches . . .	86·2	,,	9·1	0·6
Dried dates . . .	14·6	,,	63·9	2·0
Haricot beans . . .	7·9	,,	45·5	21·4
Bread	24·0	0·8	59·3	8·1
Honey	23·0	Trace	76·4	0·4

of sucrose, casein, McCollum's salt mixture No. 185 (McCollum, Rask and Becher, 1928) and dried yeast (Glaxo debittered yeast), which were incorporated in agar or gelatine gels. McCollum's salt mixture and Glaxo dried yeast had been used as satisfactory sources of inorganic salts and growth factors by Fraenkel and Blewett in work on insect nutrition. In order to minimise the effects of micro-organisms, the larvae were transferred to fresh food each day. Sucrose was later replaced by glucose, this being a simpler source of carbohydrate. The hygroscopic properties of sucrose were also undesirable.

The consistency of the food appeared to have an important effect on the development of the young larvae. Agar and gelatin possessed some properties which tended to make them unsuitable for controlling the consistency of the diets. Agar has a somewhat variable composition and is likely to contain growth factors. Gelatin is a protein, and would be inconvenient in investigations on amino-acid requirements. Furthermore, the consistency of the jelly formed by their solutions in no way resembles that of the normal foods of *C. hemipterus.*

The possibility of replacing agar by other substances was investigated. The incorporation of supposedly inert powders (gypsum, charcoal, talc, barium sulphate, sulphur and manganese dioxide) did not give the diets a sufficiently high capacity for holding water. With only about 50 per cent. water present they were undesirably liquid. Furthermore, any change in the water content of the diet was reflected as a change in consistency. Two derivatives of cellulose (I.C.I. products then known as "Cellophas WLD" and "Cellophas WFZ") proved to be very suitable stiffeners of the diets. Throughout the main part of the work "Cellophas WFZ," now known as "Cellophas B," has been used to control consistency. These products are made in three grades of viscosity and the highest was used in this work.

"Cellophas B" is an ester of cellulose which absorbs water. The consistency of the medium depends on the concentration of "Cellophas" present. Lower concentrations produce a viscous liquid, whereas higher concentrations give a stiff jelly. It was thus possible to obtain a much wider range of desired consistencies than had been possible with agar. The liquefaction of agar gels under the influence of heat (during autoclaving) was a marked disadvantage, since settlement of the solid food components tended to occur. Foods prepared with " Cellophas B " do not liquefy when heated. In much of the experimental work the foods contained about 50 per cent. solid matter. Under the conditions the Cellophas tended to retain its soft fibrous nature, thus producing a consistency which tended to resemble that of the more natural foods of *Carpophilus*. Diets prepared with " Cellophas B " can be rolled out into relatively thin sheets. Such foods should prove of value in the investigation of the nutrition of leaf-feeding insects.

It appeared that *Carpophilus hemipterus* was unable to use the " Cellophas " as a source of carbohydrates. Two foods, S and SG, were prepared having the composition shown in Table II. It will be noticed that the two diets were identical except that the glucose in diet SG was replaced by " Cellophas " in diet S. Fifteen-day-old larvae were placed on portions of each food and kept in a saturated atmosphere at 25° C. When not in use the diets were kept in a refrigerator. The larvae were transferred daily to new supplies freshly removed from stock. This was one of the early experiments, and it was not done under sterile conditions. The larvae were weighed after they had been on the foods for 6 days and the results are given in Table III. They suggest that the larvae were unable to utilise the " Cellophas." As " Cellophas " is used in foods prepared for human consumption, it is unlikely to have any toxic effect.

TABLE II.—(*Experiment* 108.)

Component of food.	Diet S.	Diet SG.
Casein	8 parts	8 parts
Cellophas B	20 ,,	.
Glucose	.	20 parts
Yeast	7 parts	7 ,,
Cholesterol	2 ,,	2 ,,
McCollum's salt mixture	2 ,,	2 ,,
5 per cent. Cellophas solution	117 ,,	117 ,,

TABLE III.—*Effect of replacing glucose in a diet by " Cellophas B "* (*Experiment* 108).

Diet.	Number of larvae surviving.	Average weight of larvae.
S	3	0·20 mg.
SG	10	2·29 ,,

c. *The Preparation of Artificial Foods.*

All the foods prepared were made as homogeneous as was practicable in order to prevent the larvae feeding on selected particles of a favoured component. The basis of many of the diets used was known as mixture T, and it had the following composition :

Casein (low vitamin content)	19 parts
Glucose (anhydrous)	41 ,,
Cholesterol	4 ,,
McCollum's salt mixture (185)	4 ,,

The components were weighed out, mixed, and dried at about 80° C. They were then ground overnight in a small ball mill. This reduced the mixture to the consistency of face-powder. A stock of mixture T was prepared and it was replenished as required.

In general the artificial foods were prepared as wet and dry fractions which were mixed just before use. The wet fraction consisted of "Cellophas B," to which had been added such components as the B-group vitamins, tryptophane, thymine, aqueous yeast extracts and any necessary water. This fraction was always allowed to stand overnight so that the "Cellophas" might absorb water evenly. The dry fraction contained such components as Food T, yeast residues, yeast nucleic acid, etc. Vitamin E and alcoholic extracts were added to the dry fraction. Their distribution through the fraction was aided by the addition of excess alcohol. This was driven off by drying the fraction overnight.

In the later experiments at least 20 per cent. of the dry fraction consisted of charcoal. Without the addition of charcoal the foods had a clay-like consistency. After being autoclaved they tended to have a thin film of superficial moisture which was not reabsorbed. This moisture was detrimental to the young larvae. Incorporation of charcoal into the foods rendered them more porous and the moisture film was rapidly reabsorbed.

After the wet and dry fraction of the food had been mixed they were kneaded by hand for about ten minutes.

Small specimen tubes (2 in. × $\frac{1}{2}$ in.) were used for the feeding experiments, and they were made up in batches of about 20. A small pad of the food was flattened on the bottom of each tube, and the remainder of the food was rolled out into long cylinders by hand. Inch lengths were broken off these cylinders and dropped into the feeding-tubes. The broken surface of the little roll of food rested on the basal food pad, and the young larvae tended to secrete themselves between the two. The tubes were closed with rubber bungs, each containing a hole plugged with cottonwool, and sterilised in an autoclave for 30 minutes at a steam pressure of 14 lbs. per square inch.

d. *Sterilisation and Transference of Eggs to Sterile Food.*

Some difficulties were experienced in devising a reliable technique for rearing the larvae under sterile conditions. The following technique was ultimately adopted.

Sterilisation was performed in the glass sterilising tubes shown in fig. 1. A pair of such tubes was used for each batch of eggs. Each sterilising tube consisted of two separate pieces of glassware joined by rubber tubing. The rubber tubing was closed by a pinch clip. Of each pair used, one was half filled with distilled water, the other left empty. Both ends of the tubes were plugged with cotton-wool and they were then sterilised in the autoclave After cooling they were supported on retort stands.

Eggs, which had been laid within the previous 24 hours, were washed by being placed in tap-water for about 5 minutes. The water was then replaced by White's sterilising fluid[2] to which a little bile salt had been added. The presence of the bile salt ensured that the eggs were thoroughly wetted, and that they did not float on the surface of the fluids used during sterilisation. As soon as the water had been replaced by sterilising fluid, the eggs were transferred by means of a pipette to the empty sterilising tube. Further sterilising fluid was added to this tube until it was about three-quarters full. The eggs sank to the bottom of the tube and rested in the rubber tubing just above the pinch clip. Any eggs that stuck to the upper part of the tube could generally be dislodged by twisting the tube sharply. The cotton-wool plug was removed for as short a time as possible during the transfer of the eggs. The eggs were allowed to remain in this tube for 25 minutes before being transferred to the second tube.

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[2] White's sterilising fluid has the following composition: $HgCl_2$, 0·25 gm.; NaCl, 6·5 gm.; concentrated HCl, 1·25 c.c.; C_2H_5OH, 250 c.c.; water, 750 c.c.

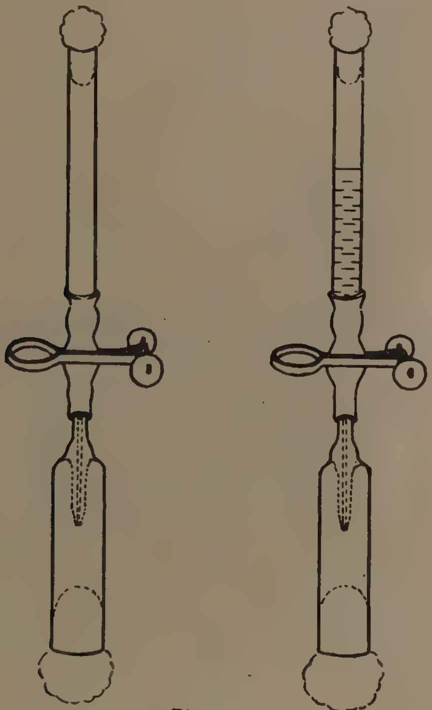

FIG 1

Fig. 1.—A pair of sterilising tubes as prepared for the sterilisation of the eggs. The upper part of each tube consisted of ¾ in. glass tubing and was tapered at the lower end. The lower part consisted of a glass jet fused into a bell of wide glass tubing. The total length of each tube was about 9 in.

Eggs were transferred to the second tube in the following manner: The cotton-wool plug was removed from the protecting bell of the first tube, discarded, and the bell flamed. The upper cotton-wool plug of the second tube was then temporarily removed and the upper part of this tube flamed. The second tube was then quickly inserted into the protecting bell of the first and the eggs transferred by opening the pinch clip. The tube now containing the eggs was withdrawn. The upper end was again flamed and the cotton-wool plug replaced. Owing to the narrow bore of the receiving tube and the difference in specific gravities, the water present in the tube and the sterilising fluid introduced with the eggs tended not to mix. The eggs were therefore rinsed as they sank through the lower layer of water.

Petri dishes containing pads of dry filter-paper were sterilised by autoclaving. The eggs were squirted onto the filter-paper pads under sterile conditions. The filter-paper absorbed the excess liquid, leaving the eggs in a clean and relatively dry condition. They were then transferred to the tubes of sterile food by means of sterile paint brushes. These paint brushes were permanently embodied in cotton-wool plugs, which were fitted into test-tubes and sterilised in the autoclave. At first only five eggs were placed in each tube of food. Later the number was increased to eight. Each sterile paint brush was used to transfer the eggs to three successive tubes before being discarded for re-sterilisation.

The transference of the eggs to the food tubes was carried out under a simple glass shield which was open at both ends. The upper end of a feeding tube was flamed, together with the arms of a pair of forceps that had been dipped in alcohol. Under the glass shield the bung was removed from the tube. The forceps gripped the bung automatically, and by resting them on a small block it was possible to support the bung free from contact with the bench. It was found most convenient to rest the tube in a sloping position in a rubber ring. The eggs were then gently transferred from the petri dish to the tube, care being taken not to raise the lid of the petri dish any more than was absolutely necessary. The sterile paint brush and cotton-wool plug were returned to their test-tube and the bung replaced in the feeding tube. The end of the feeding tube was again flamed, and then the junction between the rubber bung and the glass was sealed with molten paraffin wax. Each bung was perforated by a hole, which was tightly packed with cotton-wool. This allowed gaseous exchange to take place between the inside and outside of the tube but prevented the entry of bacterial spores, etc.

Provided that the feeding tubes were effectively sterilised after their initial preparation, the amount of bacterial and fungal contamination appearing in experiments set up in this fashion was less than 1 per cent. of the tubes used. Higher rates of contamination, which occurred at first, were found to be due to inadequate autoclaving of the feeding tubes during their preparation. After receiving the eggs, the tubes were kept in a desiccator over saturated sodium carbonate solution. This maintained a relative humidity of about 95 per cent., which prevented undue evaporation of water from the foods. At higher humidities a film of moisture was formed over the tubes and permitted the growth of moulds on the surface of the glass. Hyphae were then able to penetrate the cotton-wool plugs and infect the feeding tubes. Any differences in larval growth did not really become significant until the eighth day. By this time any tubes that were contaminated by micro-organisms could be easily detected, either by sight or by smell. Plating out the contents of different tubes on nutrient agar and glucose agar plates confirmed that, by the eighth day, contamination was only present in those tubes in which it was evident to the senses.

About 150–200 eggs constituted a conveniently sized batch for sterilisation at any one time, larger batches tending to clog the jets of the sterilising tubes.

Transferring these eggs from the petri dish might involve raising the lid some 70 or 80 times, and no doubt some spores entered the dish. In order to enter the feeding tube, however, such spores would have to settle either on, or very close to, the eggs themselves. The eggs occupied only a minute fraction of the total area of the filter-paper pads.

Brief mention may be made of two other methods of sterilisation which were used in the earlier experiments. In the first method batches of five eggs were placed in short lengths of glass tubing, one end of which was closed with muslin. They were placed in sterilising fluid for 20 minutes, transferred to distilled water, and finally placed on the food. The lengths of tubing were handled with sterile forceps. This method was not very reliable : possibly the sterilising fluid did not penetrate between the fibres of the muslin. The second method was one which was reported to have been successful when applied to Nematode eggs. The eggs were stuck in rows on adhesive cellophane tape, and the tape was dusted with talc to remove the stickiness from the rest of the surface. The tape was cut into sections, each containing five eggs. These were sterilised and washed as in the previous method. In practice neither of these methods proved as convenient or as reliable as the slightly more elaborate method finally adopted.

e. *Recording the Experimental Results.*

At first the nutritional values of the various foods were compared by observations of the length of the larval stage. Later it seemed preferable that actual growth curves should be made. Each test on a food consisted of about 20 tubes. At 3–4-day intervals throughout the test two or three tubes were withdrawn and the larvae they contained weighed and discarded. On occasion it was felt that too few larvae were available to give a very reliable figure for the average weight. Supplies of tubes had to be conserved so that future recordings could be made. In some experiments the larvae on any particular food appeared to be the same size. In a few, however, larvae of very different sizes could be found in the same tube. The reason for this was not clear. Since it seemed to occur in whole experiments rather than individual foods, and since all the eggs used in any one experiment were obtained from the same batch of adults, it may have been due to mixed potentialities in the eggs. Reynolds (1945) has shown that the growth of *Tribolium destructor* larvae may be influenced by the parental diet. This may have occurred in some overcrowded cultures of *Carpophilus*. Larval ages were calculated from the dates on which the eggs were laid. At 25° C. *Carpophilus hemipterus* eggs hatch within 48 hours of being laid. The growth curves were all assumed to start from a larval weight of 0.5 mg. on the second day (the day of hatching).

III. SOME EFFECTS OF MICRO-ORGANISMS ON THE NUTRITION OF *CARPOPHILUS HEMIPTERUS*.

Under septic conditions the larvae grew well on various diets containing mixture T, dried yeast, and " Cellophas B " solution. In order to minimise the effects of micro-organisms, the bulk of the prepared food was sterilised in the autoclave and then kept in the refrigerator. Small portions were removed each day and the larvae transferred on to these. Then the dried yeast in the food was replaced by extra mixture T and a " vitamin mixture " growth was still normal. The "vitamin mixture" contained those factors known or suspected to be of importance in insect nutrition. They were thiamin, riboflavin, nicotinic acid, pantothenic acid, pyridoxin, biotin, *p*-amino benzoic acid, inositol, folic acid, tryptophane, thymine, yeast nucleic acid, ergosterol, and α-tocopherol acetate. It became evident, however, that micro-organisms were interfering to such an extent as would invalidate any results that might be obtained. It was therefore necessary to devise a simple sterile technique, and an account of that finally adopted has already been given.

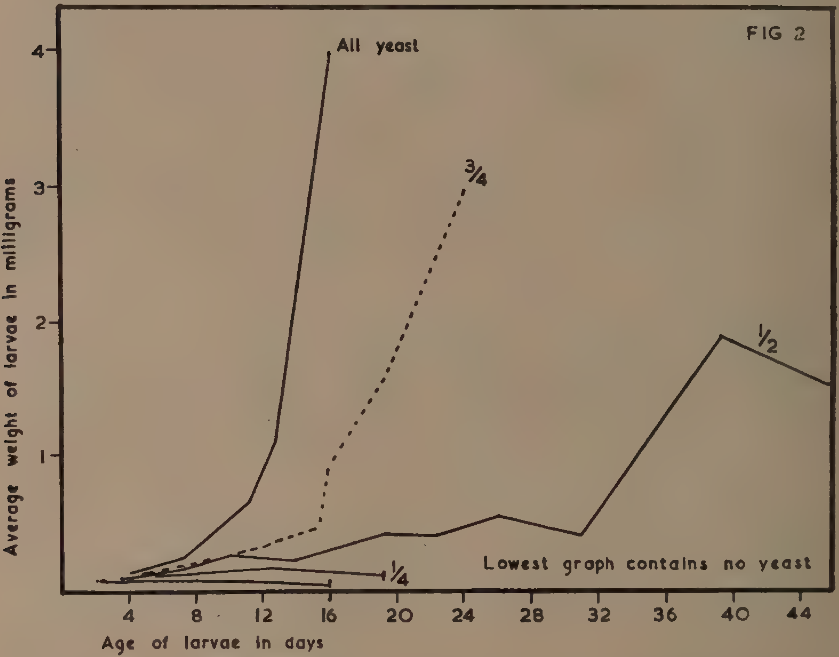

Fig. 2.—The effect of the yeast content of an artificial food on the rate of growth of the larvae. The numerical fraction shown by each growth curve indicates the proportion of yeast present in the dry fraction of each diet. One curve has been dotted to avoid confusion with neighbouring curves. The short vertical line at the end of a curve indicates the death of the larvae concerned.

When reared under sterile conditions the yeast requirement of the larvae was found to be much greater than had been expected. Foods were prepared that contained 50 per cent. "Cellophas B" solution and 50 per cent. of a mixture of mixture T and yeast. The proportion of yeast present was varied. The growth curves of larvae reared on these foods are given in fig. 2. The numerical fractions shown against each curve refer to the proportion of dried yeast present, e.g., $\frac{3}{4} = 75$ per cent. yeast + 25 per cent. Food T. It will be noted that growth was very slow even when half the dry fraction was supplied as yeast. This result was probably due, at least in part, to a deficiency in yeast of one or more of the known growth factors, since the addition of "vitamin mixture" to this 50 per cent. yeast food converted it into an adequate diet.

Of the foods used in this experiment, growth was most rapid on that composed entirely of yeast. Throughout the entire work under sterile conditions, however, no food was found on which the larvae would grow as rapidly as they did when they had access to living fungi. On one occasion, when larvae eleven days old which had been living in a contaminated tube were weighed, their average weight was 4.73 gm. This figure indicates how inferior the artificial foods were when compared with some natural foods.

The more rapid growth rates that occurred with living fungi may have been due to a lack of certain factors in the dried yeast or to their destruction during the preparation of the foods. Consideration of fig. 3, which shows the effect of the water content of the food on the growth rate, suggests that such a great difference in the rate of growth would not result entirely from the higher water content of the living fungi.

The results shown in fig. 2 suggested that dried fruit might not be a nutritionally adequate diet for the larvae. This was shown to be so for the normal culturing medium of boiled dates. It was not possible to rear the larvae on boiled dates under sterile conditions. They died without showing any signs of growth. When dried yeast was incorporated with the sterile dates growth occurred, and half the larvae had pupated by the 20th day. When the boiled dates were sterilised and then left open to the air for recontamination successful growth again occurred, but pupation was somewhat delayed. In this case development was slow and mortality high in the beginning, due, perhaps, to the time required by fungi to establish themselves in the medium. It seems likely that rapid development of the larvae under natural conditions depends on the presence of certain micro-organisms, especially fungi.

IV. EFFECT OF WATER CONTENT OF FOOD ON RATE OF GROWTH OF LARVAE.

It has been shown that the rate of growth was relatively rapid on a diet of dried yeast and " Cellophas B " solution. In order to determine the effect of the water content of the food on the rate of growth, simple food mixtures of dried yeast and " Cellophas B " solution were prepared. The water contents of the foods were obtained in the usual way by drying to a constant weight.

The growth curves of the larvae used in this experiment are shown in fig. 3. It will be noted that the differences between the growth curves are small, except for that containing only 34 per cent. water. Growth on this food was considerably slower than on the others. Results indicate that reduction of the water content below 34 per cent. would probably slow down the rate of larval growth considerably. Reduction in the growth rate was accompanied by an increase in mortality (Table IV) on the dried foods.

TABLE IV.—*Mortality rate of larvae reared on diets of different water contents.*

Percentage water in food.	Eggs placed on food.	Larvae present on 16th day.	Percentage mortality.
34	35	9	74
45	25	23	8
52	30	23	23
62	25	25	0
73	20	20	0
83	20	20	0

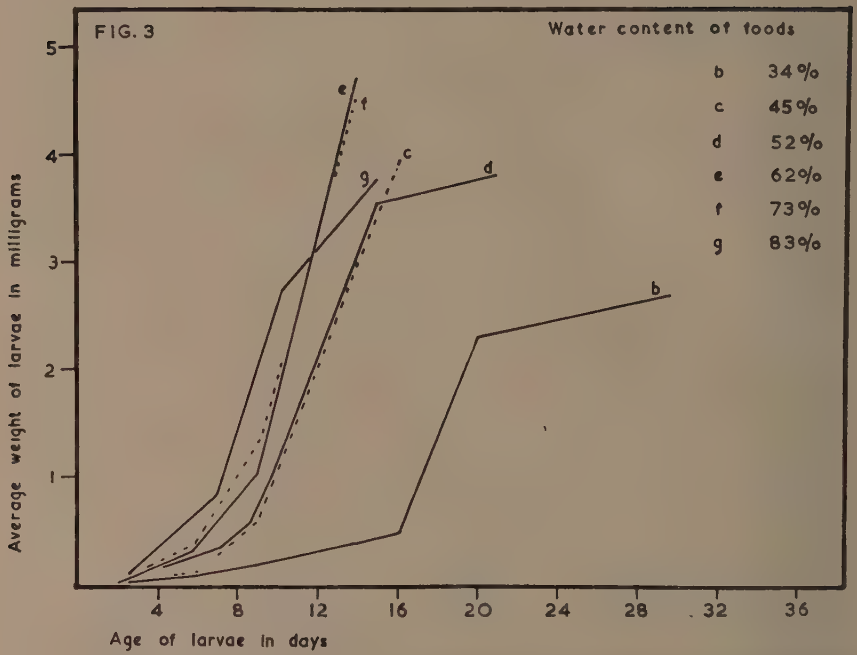

Fig. 3.—The effect of the water content of an artificial diet on the rate of growth of the larvae.

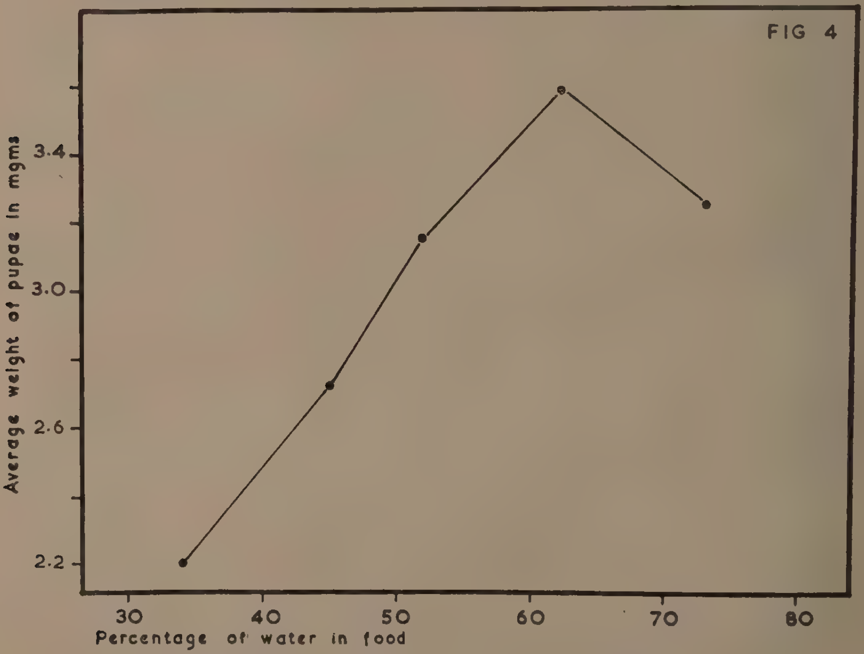

Fig. 4.—The effect of the water content of the larval diet on the size of the pupae.

The size of the pupae varied with the water content of the food on which the larvae were reared. This is apparent from fig. 4, where the average weight of the pupae is plotted against the water content of the food. No pupae were produced by the larvae on the wettest food, despite the rapid rate of growth. This may have been due to unfavourable physical conditions, this food being rather softer than the others, so that quiescent pupating larvae tended to sink into it and were presumably asphyxiated.

From the evidence presented above, it would seem that *Carpophilus hemipterus* might have difficulty in establishing itself in foods containing less than 30 per cent. water. According to the figures quoted in Table I, however, the water contents of several types of dried fruit known to be attacked by *C. hemipterus* are considerably lower than this. Field observations might show that the beetle is only able to establish itself in dried fruit that is in good condition if the water content is sufficiently high. It is, perhaps, significant that attempts to culture the beetle on raisins, as obtained from store, failed. When the raisins had been soaked, however, they became very suitable.

V. UNIDENTIFIED WATER-INSOLUBLE FACTORS PRESENT IN DRIED YEAST.

Under sterile conditions the larvae thrived on a variety of food mixtures containing mixture T, dried yeast, and " Cellophas B " solution, provided that the amounts of yeast and water present were relatively high. When the dried yeast was replaced by the further addition of mixture T together with synthetic growth factors no growth of the larvae occurred. This result was not affected by doubling the amount of the synthetic growth factors present. The failure of the yeast-free diet was, therefore, not primarily due to a deficiency of one of the added growth factors. The factors added included all those factors that had been isolated, and that were known or suspected by 1950 to be of nutritional importance to some insects, except such substances as would be supplied in mixture T, e.g., amino-acids. The added factors were thiamin, riboflavin, nicotinic acid, pantothenic acid, pyridoxin, biotin, *p*-amino benzoic acid, inositol, folic acid, tryptophane, thymine, yeast nucleic acid, cholesterol, ergosterol and α-tocopherol acetate.

When a tube containing a yeast-free diet of mixture T, added growth factors, and " Cellophas B " solution became accidentally infected with living fungi, larval growth was very rapid. There was, therefore, no deficiency of inorganic material in the diet.

Experimental work indicated that yeast contained one or more factors, insoluble in water or alcohol, that were of nutritional importance to *Carpophilus hemipterus*. In separate experiments yeast was extracted with water, alcohol, and water/alcohol mixtures. In each case the resulting extract and residue were incorporated, both separately and together, in artificial diets containing mixture T, the synthetic growth factors, charcoal, and " Cellophas " solution.

Rather similar results were obtained in every case, and it is only necessary to describe one of the experiments in any detail. In this experiment the solvent used was 50 per cent. methanol ; 2 litres of 50 per cent. methanol were added to 200 gm. of dried yeast. The mixture was stirred vigorously for 4 hours, allowed to stand overnight, and then filtered. The yeast residue was suspended again in a further 1½ litres of the solvent and stirred for two hours. After filtering, the residue was suspended once more in 1½ litres of 70 per cent. methanol and stirred for an hour. It was then filtered again, and the yeast residue was dried at 60° C. and ground to a fine powder in the ball mill. A 300 ml. portion of the first filtrate was concentrated to 30 ml. by evaporation under reduced pressure; 1 ml. of this concentrate was equivalent to the extract from 1 gm. of dried yeast.

The above procedure was varied slightly in some of the other experiments. If the extraction was carried out with water the resulting slurry did not filter easily and had to be separated by centrifuging. Sometimes all the extracts were bulked before concentration.

The composition of the foods used in this experiment is given in Table V.

TABLE V.—*Composition of foods used in Experiment* 138.

Component.	Diets.			
	a. With yeast.	*b.* Residue + extract.	*c.* Residue only.	*d.* Extract only.
Saturated choline chloride solution	0·1 ml.	0·1 ml.	0·1 ml.	0·1 ml.
Biotin, in 1 ml. water	100 µg.	100 µg.	100 µg.	100 µg.
Ergosterol	25 mg.	25 mg.	25 mg.	25 mg.
Yeast nucleic acid	400 ,,	400 ,,	400 ,,	400 ,,
α-tocopherol acetate solution*	0·25 ml.	0·25 ml.	0·25 ml.	0·25 ml.
" Vitamin Mixture "	10 ,,	10 ,,	10 ,,	10 ,,
Water	12·5 ,,	2·5 ,,	12·5 ,,	2·5 ,,
Mixture T	10·0 gm.	10·0 gm.	10·0 gm.	10·0 gm.
Dried yeast	10·0 ,,			
Yeast extract		10·0 ,,		
Yeast residue		10·0 ,,	10·0 gm.	
Charcoal	5·0 gm.	5·0 ,,	5·0 ,,	15·0 gm.
"Cellophas B"	2·5 ,,	2·5 ,,	2·5 ,,	2·5 ,,

* Alcoholic solution containing 3·4 mg./ml.

TABLE VI.—*Composition of " vitamin mixture " used in Experiment* 138. *Quantity of synthetic growth factors dissolved in* 50 *ml. of solution.*

Thiamin	5 mg.
Riboflavin	5 ,,
Nicotinic acid	5 ,,
Pantothenic acid	5 ,,
Pyridoxin	5 ,,
p-aminobenzoic acid	5 ,,
Inositol	500 ,,
Folic acid	5 ,,
Thymine	10 ,,
Tryptophane	250 ,,

The components of the " vitamin mixture " are listed in Table VI. In order to dissolve the latter, it was necessary to warm the solution and add a few drops of concentrated sodium hydroxide solution.

The growth curves obtained from this experiment are shown in fig. 5. It will be noted that the total nutritional value of the yeast was not altered as a result of the extraction, the curve obtained from the food containing yeast residue and extract resembling that obtained from the control food containing yeast. Growth occurred on the diet containing the yeast residue. Growth on the diet containing the extract was much slower. In this particular experiment the amount of edible material in the extract diet was considerably less than in the other diets, the solid content of the food having been maintained by the addition of charcoal. The same result, however, was obtained from experiments in which an extra amount of T was added to maintain the desired water : solid ratio. Usually the larvae feeding on the extract diet showed less growth than they did in this experiment and died about three weeks after hatching.

FIG. 5

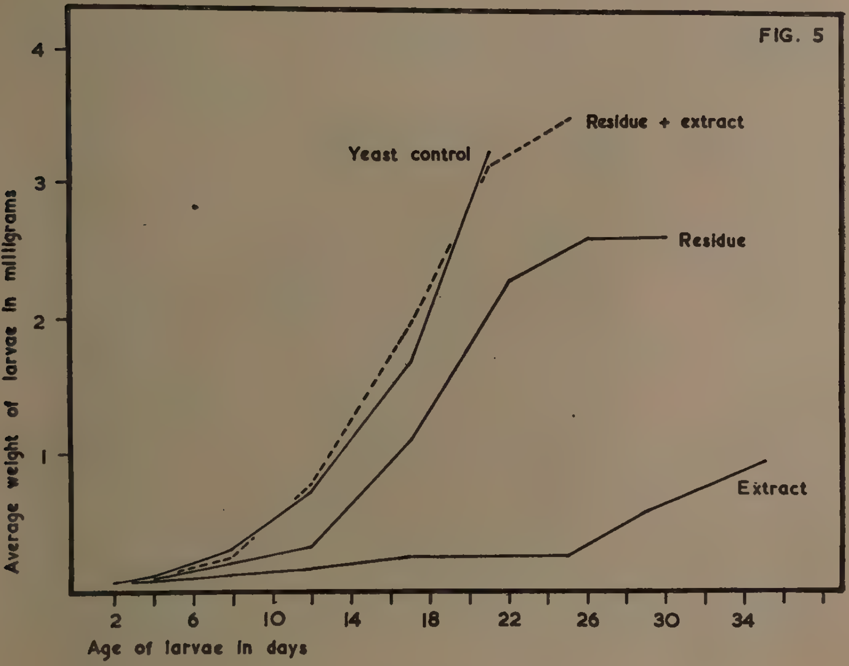

Fig. 5.—The extraction of yeast with 50 per cent. methanol. (*For explanation see text.*)

In experiments on the solubility of the unidentified factor three separate batches of yeast were extracted with solvent. One batch of yeast received only one extraction, the second batch received two successive extractions and the third batch received three extractions. Equal amounts of solvent were used for each extraction. The extracts from the different batches of yeast were kept separately, but those from the same batch were added together. After concentration the extracts were added to diets rather similar to that described in Table V, column d, except that they contained 20 gm. food T and 5 gm. charcoal. Had the unidentified factor been slightly soluble, larvae on the food containing the three extracts should have grown faster than those on the food containing only one extract. Fig. 6 (Experiment 149) gives the growth curves obtained when 70 per cent. ethanol was used as the solvent in this type of experiment. They do not indicate any solubility of the factor in this solvent. On one occasion a slight solubility in water was suggested by the results obtained. When water was used, however, the extracts had to be separated by centrifuging. As a result some finely divided insoluble material may have been carried over into the extract.

It seemed, therefore, that dried yeast contained a water-insoluble factor of importance in the nutrition of *Carpophilus hemipterus*. Further experiments indicated that the factor was also insoluble in ethanol, petroleum ether (40°–60°), chloroform, or acetone.

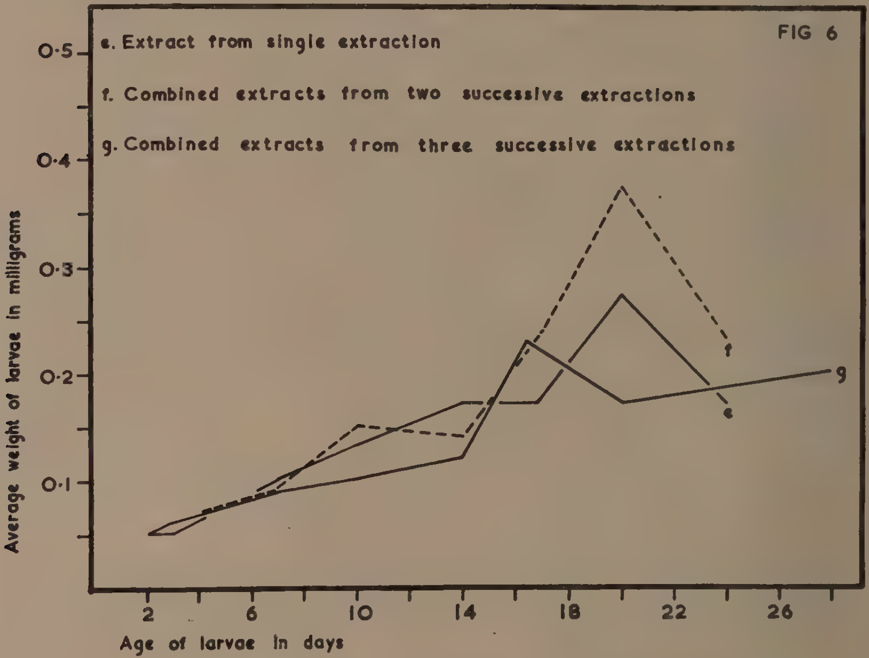

Fig. 6.—The successive extraction of yeast with 70 per cent. methanol. (*For explanation see text.*)

Begg and Robertson (1950) reported the existence of an acid-insoluble, but alkali-soluble, factor in yeast that was important in the nutrition of *Drosophila melanogaster*. They were able to prepare an active precipitate from live yeast which contained this factor. The yeast was boiled for 15 minutes with 2 per cent. sodium bicarbonate. After filtering off the residue, an active precipitate was obtained by treating the filtrate with acid and alcohol. In my work on *Carpophilus hemipterus* dried yeast was twice extracted with 70 per cent. methanol acidified with hydrochloric acid. This, presumably, would have removed much water-soluble material but not the factor of Begg and Robertson. The residue from the acid-alcohol extraction was stirred for three hours with 1 per cent. ammonium hydroxide and centrifuged. The supernatant liquid was withdrawn, and sufficient alcohol added to it to give a concentration of 70 per cent alcohol. On acidification with 5 per cent hydrochloric acid a voluminous white precipitate appeared. This was removed by centrifuging, washed with acid alcohol, dried, and ground to a fine powder. It contained about 8 per cent. of the original solid matter of the yeast, and was embodied, in place of yeast residue, in a diet similar to that shown in Table V, column c. One gramme of dried precipitate + 9 gm. of charcoal were used to replace 10 gm. of yeast residue. On such a diet the larvae showed no signs of growth and died within about three weeks. It seemed unlikely that the missing factor was that of Begg and Robertson. Later evidence, however, indicated the possibility of two factors being present in the water-insoluble yeast residue. If this is so, one of them may have been present in the precipitate obtained. In the absence of the other factor the precipitate would not sustain growth.

The evidence suggesting that two factors may be present in the yeast residue will now be presented.

It was possible that the insoluble factor was either a component of, or chemically bound to, the yeast protein. In either case digestion with a proteolytic enzyme might be expected to render the factor water-soluble. Digestion with pepsin proved to be unsatisfactory. Owing to the great buffering capacity of the yeast, it was necessary to add large quantities of hydrochloric acid in order to maintain a suitable pH for the action of the enzyme. Complications were thus added to the feeding experiments, and to the interpretation of the results obtained. Papain proved to be a very suitable enzyme, having an optimum pH of about 5.6. This was near to the pH automatically attained by the yeast as a result of the proteolytic digestion. It was not necessary, therefore, to add chemicals to adjust the pH.

The growth curves obtained from two experiments involving papaic digestion of the yeast are shown in fig. 7 (Experiment A) and fig. 8 (Experiment B). These two experiments were set up in similar fashion, except that some hydrogen peroxide was added to the yeast used in Experiment B. This peroxide was intended to inhibit the action of the enzyme in B, and allow an estimate to be made of the extent to which digestion had proceeded in A. Such a control might also enable any effects due to the presence (rather than the digestive action) of papain to be detected. As will be shown, little inhibition of the enzyme occurred, and it seems justifiable to quote Experiment B as a duplicate of Experiment A.

Digestion was carried out with the following mixtures for 18 hours at 60° C. :

	Experiment A.	*Experiment B.*
Dried yeast . . .	30 gm.	30 gm.
Papain . . .	0·3 ,,	0·3 ,,
H_2O_2 (20 vols.) .	·	2·0 ml.
Water . . .	120 ml.	120 ml.

After digestion the mixture formed a viscous slurry. 100 ml. of water were added to each digest, which was then centrifuged for an hour at 2500 r.p.m. After removing the supernatant fluid each digest was washed twice by resuspension in water followed by separation by centrifuging. Finally each digest residue was suspended twice in absolute alcohol, filtered, and dried. The loss in weight of the yeast in A and B was 65 per cent. and 57 per cent. respectively.

Water extraction of the dried yeast normally reduced the dry weight by about 10 per cent., so that the loss due to the action of papain on these two samples was about 55 per cent. and 47 per cent. A previous Kjeldahl analysis on the yeast residue after water extraction had given the figure of 52 per cent. as the protein content of the residue. The papain had apparently converted most of the protein into soluble material.

The details of the foods tested in this experiment are given in Tables VII and VIII. Food " a " was a control containing yeast. Foods " b " to " g " contain the digest residues, and extracts. Food " h " is a control containing mixture T and the synthetic growth factors. Food " i " was similar to the control " a," except that papain was added to it in the final stages of its preparation. It would have shown any detrimental effects due to the presence of the enzyme. An attempt was made to use equivalent quantities of yeast, digest residues, and digest extracts. The digest extracts contained all the liquids removed from the washing of the residue. They were concentrated by evaporation under reduced pressure before being incorporated in the foods. In preparing the foods allowances were made for the soluble solid material present in the extracts. This ensured that all the foods had similar water content, a fact that was verified by analysis.

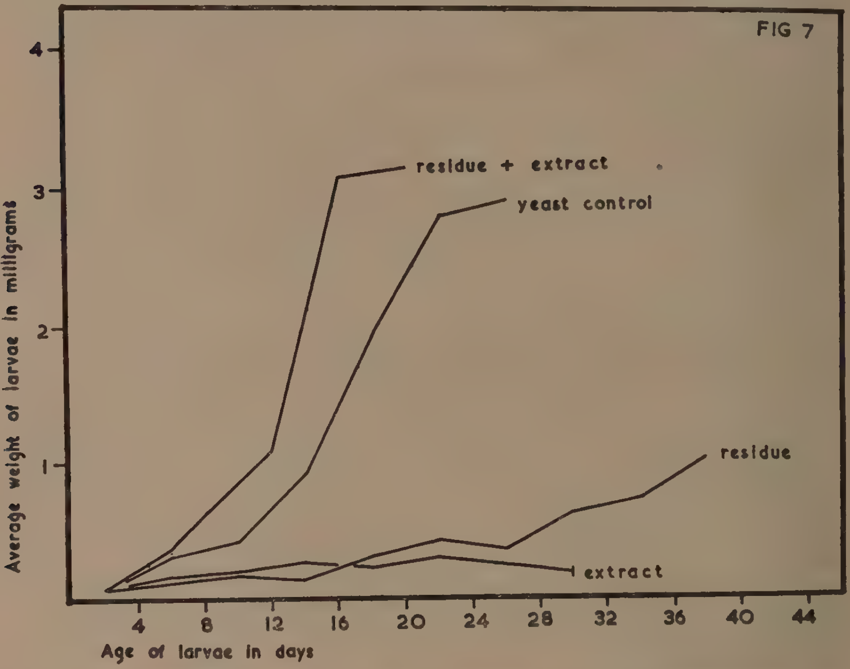

Fig. 7.—The digestion of yeast by papain (Experiment A). The digested yeast was divided into a soluble fraction (the extract) and an insoluble fraction (the residue). These were incorporated in artificial diets. The rate of growth on these diets was compared with a "yeast control" diet containing undigested yeast. The short vertical line at the end of the lower curve indicates the death of the larvae.

Figs. 7 and 8 indicate that by themselves both digest residues and digest extract failed to promote larval growth. When recombined in the one food, growth was apparently normal. This suggested that two factors had been present in the insoluble yeast residue, one of them becoming soluble as a result of the action of papain. The slow, but definite, growth obtained on the digest residue diet seems to indicate that both factors were present in the residue to some extent. This may have been the result of incomplete washing of the residue to free it from the products of digestion.

A second interpretation of these results is available. It is possible that the original yeast contained only one factor, but that it was present in adequate quantities to promote larval growth. After digestion this factor may have become divided between the two fractions so that neither fraction contained enough of it to support growth.

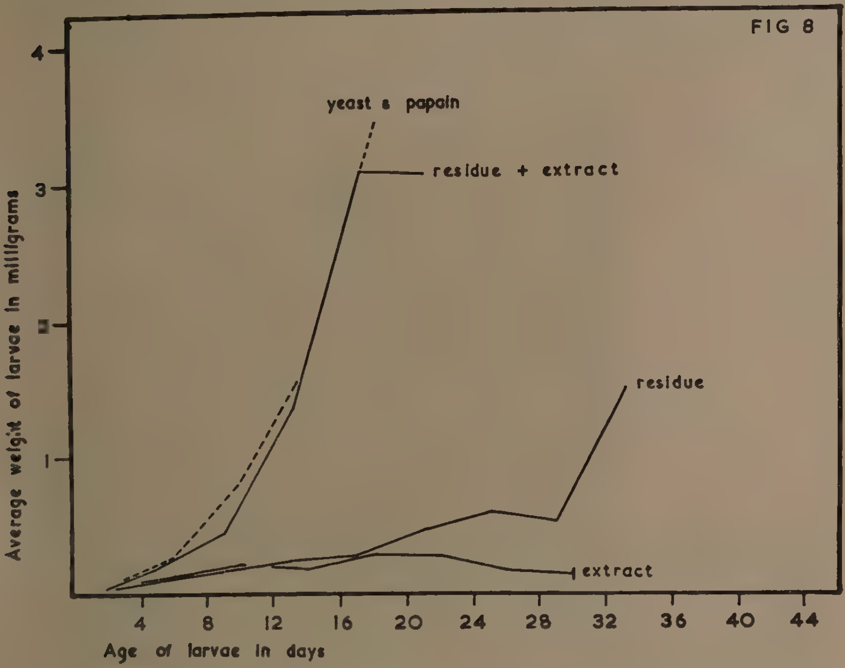

Fig. 8.—The digestion of yeast by papain (Experiment B). This experiment was essentially similar to that shown in fig. 7. The dotted line represents growth on a diet containing yeast to which papain was added in the final stages of preparation, i.e., just before autoclaving. Little proteolytic action is likely to have taken place in this diet. The short vertical line at the end of the lower curve indicates the death of the larvae.

The experiment also provides evidence against the idea that the beneficial effect of yeast residue is due to its " taste," which stimulates the larvae to eat more—unless one postulates the existence of two such " tastes " that have to be present together.

TABLE VII.—*The composition of foods used to determine the effect of papaic digestion on the nutritive properties of yeast.*

	a.	*b.*	*c.*	*d.*	*e.*	*f.*	*g.*	*h.*	*i.*
Mixture T	10 gm.	10 gm.	20 gm.	10 gm.	10 gm.	20 gm.	10 gm.	20 gm.	10 gm.
Dried yeast	10 ,,	.	.	.	.	.	.	.	10 ,,
Digest residue "A"	.	3·5 gm.	.	3·5 gm.	.	.	.	.	.
,, ,, "B"	.	.	.	.	4·3 gm.	.	4·3 gm.	.	.
,, extract "A"	.	.	17 ml.	17 ml.	.	.	.	.	.
,, ,, "B"	.	.	.	.	.	16 ml.	16 ml.	.	.
Charcoal	5 gm.	5 gm.	5 gm.	5 gm.	5 gm.	5 gm.	5 gm.	5 gm.	5 gm.
Yeast nucleic acid	0·3 ,,	0·3 ,,	0·3 ,,	0·3 ,,	0·3 ,,	0·3 ,,	0·3 ,,	0·3 ,,	0·3 ,,
Inositol	0·1 ,,	0·1 ,,	0·1 ,,	0·1 ,,	0·1 ,,	0·1 ,,	0·1 ,,	0·1 ,,	0·1 ,,
α-tocopherol acetate solution*	1 ml.	1 ml.	1 ml.	1 ml.	1 ml.	1 ml.	1 ml.	1 ml.	1 ml.
Food T to make up residue weight	.	6·5 gm.	.	.	5·3 gm.	.	.	.	.
"Cellophas B"	2·5 gm.	2·5 ,,	2·5 gm.	2·5 gm.	2·5 ,,	2·5 gm.	2·5 gm.	2·5 gm.	2·5 gm.
Water	15 ml.	15 ml.	12 ml.	5 ml.	15 ml.	11 ml.	5 ml.	15 ml.	15 ml.
"Vitamin Soln."	10 ,,	10 ,,	10 ,,	10 ,,	10 ,,	10 ,,	10 ,,	10 ,,	10 ,,
Papain (mixed with food in final stages of preparation)				.	.	.	.	.	0·3 gm.

* 1 ml. of alcoholic α-tocopherol acetate solution contains 7·6 mg. α-tocopherol acetate.

TABLE VIII.—*Composition of "vitamin solution" used for preparation of foods in Table VII.*

	Quantity of substance dissolved in 100 ml. of solution.
Thiamin	25 mg.
Riboflavin	25 ,,
Nicotinic acid	25 ,,
Pantothenic acid	25 ,,
Pyridoxin	25 ,,
p-aminobenzoic acid	25 ,,
Biotin	2·5 ,,
Folic acid	25 ,,
Thymine	50 ,,
Tryptophane	500 ,,

VI. EXPERIMENTS ON THE B-GROUP VITAMINS.

In order to investigate the importance of the B-Group vitamins a control food was prepared which contained mixture T, yeast residue after aqueous extraction, inorganic salts, the synthetic growth factors, cholesterol, and "Cellophas B" solution. Larval growth on this food was compared with larval growth on a similar food from which one of the synthetic vitamins of the B-Group had been omitted. In assessing the results obtained it must be remembered that, although a certain factor may have been omitted from the synthetic vitamin mixture, it may still have been supplied with the yeast residue. Figs. 9 and 10 demonstrate the growth curves obtained when the various factors were omitted.

a. *Riboflavin, Nicotinic Acid, Pantothenic Acid, Choline Chloride.*

When any of these factors were omitted from the diet the larvae did not grow after hatching. Except when choline was omitted, death occurred in about two weeks. When choline was omitted, the larvae still were active after five weeks although they had not grown. It was not known whether this was due to traces of choline that remained in the residue or whether, in insects, choline is associated with the processes of growth rather than those of survival.

Riboflavin, nicotinic acid and pantothenic acid are essential for the survival of *Carpophilus hemipterus* larvae. Choline is at least essential for their growth.

b. *Pyridoxin.*

When pyridoxin was omitted from the diet the larvae grew more slowly than they did on the control diet. The mortality rate was abnormally high, and nearly all the larvae had died before they attained one-third of the weight of healthy full-grown larvae. Pyridoxin is undoubtedly essential for survival.

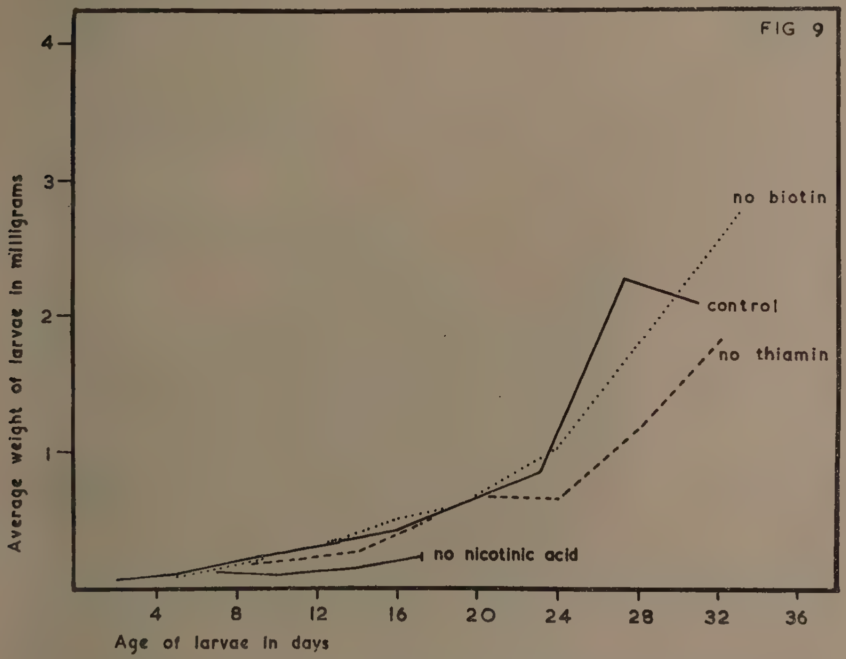

Fig. 9.—The omission of individual vitamins of the B group from an artificial diet. The short vertical line at the end of the lowest growth curve indicates the death of the larvae. Growth curves similar to this lowest curve were also obtained when either riboflavin or pantothenic acid were omitted from the diet.

c. *Thiamin.*

Omission of thiamin reduced the rate of larval growth. It is therefore at least of some importance in the nutrition of *C. hemipterus*.

d. *Biotin, p-Aminobenzoic Acid, Inositol and Folic Acids.*

Omission of these vitamins did not apparently affect the rate of growth. Since these vitamins may have been inadvertently supplied with the yeast residue, no conclusions may be made as to their nutritional importance. It is known that, although normally a water-soluble substance, biotin is " bound " to yeast in such a way that it is not extracted by water.

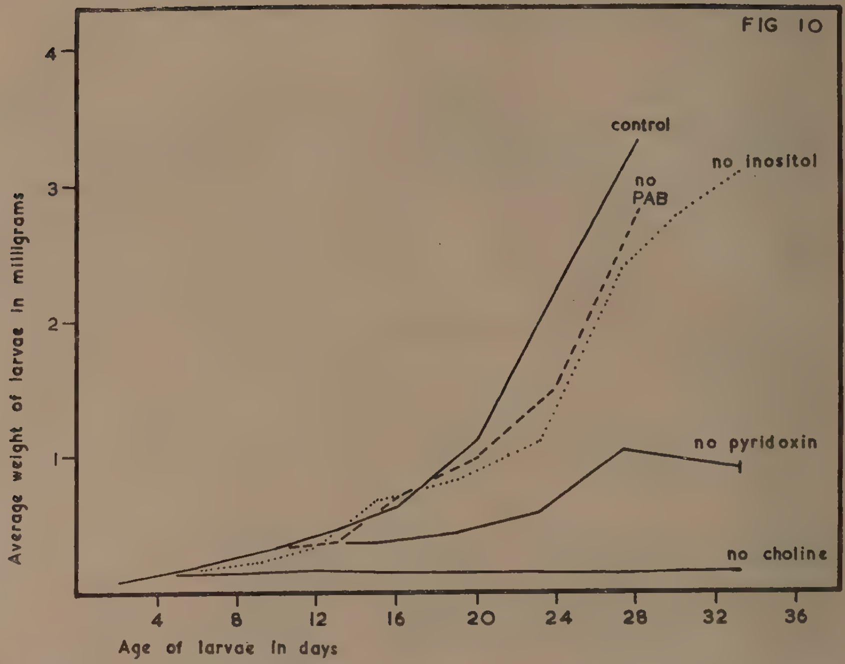

Fig. 10.—The omission of individual vitamins of the B group from an artificial diet. The vertical line at the end of the second lowest curve indicates the death of the larvae.

VII. Experiments on the Sterol Requirements of the Larvae.

A batch of dried yeast was given the following extractions in order to free it from those substances soluble in fat solvents: four with petroleum ether, two with chloroform, two with acetone, and one with methanol. In general, each extraction involved boiling under reflux for two or more hours. The resulting yeast residue only gave the slightest positive reaction when subjected to the Lieberman-Burchard test for the common natural sterols.

The residue was incorporated into diets having the composition shown in Table IX. These foods were composed basically of the yeast residue that remained after the above extractions, a modified mixture T (cholesterol replaced by charcoal), the synthetic growth factors, and " Cellophas " solution. Food " a " contained yeast in place of the yeast residue. To the other diets were added, either separately or in combination, ergosterol, cholesterol, and α-tocopherol acetate. The results are shown in fig. 11. It will be noted that the rate of growth on the supposedly sterol-free diet " b " was only a little slower than on the diet containing unextracted yeast. This was a surprising result in view of Fraenkel and Blewett's findings on the sterol requirements of some other insects (Fraenkel and Blewett, 1943). Addition of either ergosterol or cholesterol to the diet resulted, however, in faster growth. It seems that these sterols can at least be utilised by the larvae, which derive some benefit

Table IX.—*Composition of foods used to investigate the nutritional importance of ergosterol, cholesterol and α-tocopherol acetate.*

	a.	*b.*	*c.*	*d.*	*e.*	*f.*	*g.*
Modified mixture T	10 gm.	10 gm.	10 gm.	10 gm.	10 gm.	10 gm.	10 gm.
Dried yeast	10 ,,	.	.	.	.	.	.
Yeast residue	.	10 gm.	10 gm.	10 gm.	10 gm.	10 gm.	10 gm.
Yeast nucleic acid	0·3 gm.	0·3 ,,	0·3 ,,	0·3 ,,	0·3 ,,	0·3 ,,	0·3 ,,
Inositol	0·1 ,,	0·1 ,,	0·1 ,,	0·1 ,,	0·1 ,,	0·1 ,,	0·1 ,,
" Vitamin mixture "*	10 ml.	10 ml.	10 ml.	10 ml.	10 ml.	10 ml.	10 ml.
" Cellophas B "	2·5 gm.	2·5 gm.	2·5 gm.	2·5 gm.	2·5 gm.	2·5 gm.	2·5 gm.
Ergosterol	0·5 ,,	.	0·5 ,,	.	0·5 ,,	.	.
Cholesterol	0·5 ,,	.	.	1 ml.	1 ml.	.	1 ml.
α-tocopherol acetate solution (7·6 mg./ml.)	1 ml.	.	.	.	.	0·5 gm.	0·5 gm.

* The " vitamin mixture " had the same composition as that described in Table VIII.

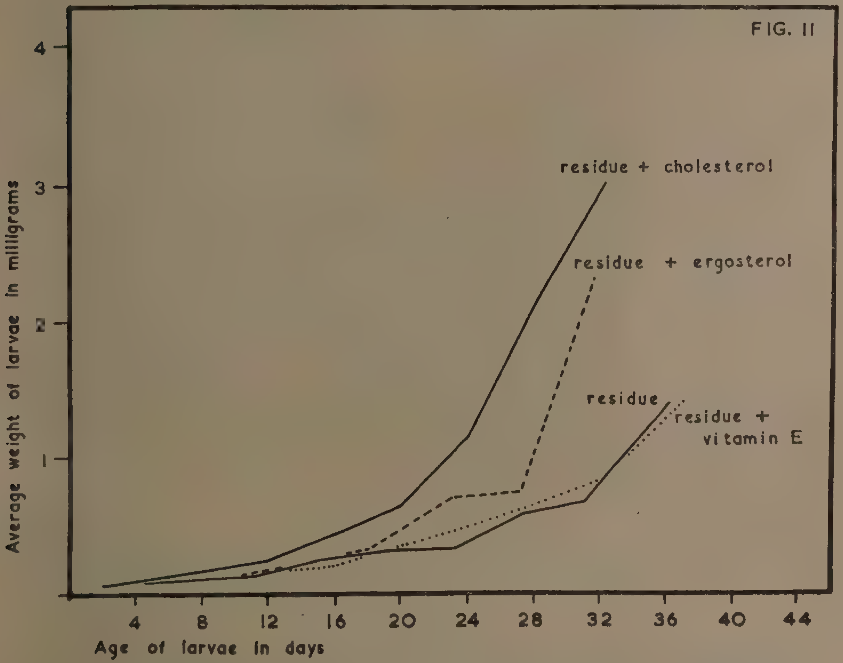

Fig. 11.—The addition of cholesterol and ergosterol to an artificial diet. Before addition of the sterols the diet had been extracted with sterol solvents until it gave a negative reaction to the Liebermann-Burchard test.

from them. The addition of α-tocopherol acetate did not appear to influence the rate of growth in any way.

The experiment was repeated with dried yeast that had been thoroughly extracted with acetone and chloroform so that it gave a negative result when tested for the presence of sterols. Similar results were obtained. Finally the diet of modified mixture T and yeast was thoroughly extracted with acetone and chloroform. The same results were obtained from feeding experiments.

The nutritional significance of ergosterol and cholesterol to *Carpophilus hemipterus* larvae is therefore uncertain. These or other sterols may be incorporated in the yeast in such a manner that they are not extracted with the usual solvents. The addition of either substance to a diet which had been extracted with sterol solvents appeared to stimulate the growth rate to a small extent.

ACKNOWLEDGMENTS.

My best thanks are due to Dr. H. E. Hinton for his advice and encouragement during the course of this work, and to Professor J. E. Harris for placing at my disposal the facilities of his Department.

SUMMARY.

1. A technique has been described for rearing *Carpophilus hemipterus* larvae on artificial diets under sterile conditions.

2. The larvae did not survive on the normal culturing medium of boiled dates unless living micro-organisms or large amounts of dried yeast were present.

3. A relatively high water content in the diet was necessary for rapid growth. On diets with a low water content the mortality rate was higher and the pupae smaller.

4. After water extraction dried yeast still contained one and possibly two factors that were apparently essential to the larvae.

5. Riboflavin, nicotinic acid, pantothenic acid were found to be essential for growth and survival of the larvae. Pyridoxin was essential for survival, and choline chloride was essential for growth.

6. On certain artificial foods the growth rate was increased by the addition of cholesterol or ergosterol.

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A STUDY OF THE LIFE-CYCLE OF *ADLERIA KOLLARI* HARTIG, THE MARBLE OR DEVONSHIRE GALL.

By Eric M. Marsden-Jones, F.L.S., F.R.E.S.

With a Revision of the Nomenclature by R. B. Benson.

Manuscript received 10th April, 1952.

(Read 3rd December, 1952.)

With 2 Plates and 9 Text-figures.

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ADLERIA KOLLARI Hartig.

Introduction into England.

How the Marble or Devonshire Gall, so called because it first made its appearance in that county, came to be introduced into this country is not known. Its arrival was probably associated with the dyeing of cloth which was manufactured in Exeter and neighbouring towns. The Aleppo gall, *Cynips tinctoria* Mayr, was imported for that purpose, and *A. kollari* may have been accidentally introduced, or imported for experimental purposes. The galls could have had no commercial value, as it is stated they contain only about 17 per cent. of tannic acid, while those of *C. tinctoria* contain over 50 per cent. Attempts to use them for ink-making also proved unsatisfactory owing to their low tannic acid content. The authentic history of the gall's appearance in Britain dates from 6th November, 1854, when Mr. Rich (1)*, present as a visitor at a meeting of the Entomological Society of London, exhibited some sprays of oak thickly covered with bunches of large galls, and stated that "they were very abundant in Somersetshire and parts of Gloucestershire." H. T. Stainton at the same meeting said "that he had noticed these galls in Devonshire but not in such profusion as now stated." At the following meeting on 4th December Stainton read an extract from a letter from R. C. R. Jordan in which he said "that he had known the galls for twenty years and that of late they had become more common." Stainton added "that since the last meeting he had ascertained that the galls were more than usually abundant in Devonshire this year." E. Parfitt (2), of Exeter, writes on 7th April, 1856, "the galls in question are stated to have been brought into notice by Mr. Rich at the November meeting of the Entomological Society. Now I believe this is incorrect; I was the first to take particular notice of them. I sent some of the galls to Mr. Westwood as far back as 1848 or 1849 to ask the name of the *Cynips* which caused these excrescences—I sent to him through the gardening periodicals, and received the name *Cynips Quercus-terminalis*."

R. C. R. Jordan (3), writing in 1871, says he noticed *C. kollari* in Devon "certainly for forty years at least (since we used the galls as marbles when I was quite a child), yet it did not reach Birmingham until 1860, when it was first noticed by me in the town—a fact not to be wondered at, considering how often its galls were brought from the south by tourists; it was not, however, until the autumn of 1866 that it was first seen by me invading Birmingham, along the hedges on the Worcestershire side; the two streams have since met, and *C. kollari* is to be found both in town and country."

James Hardy (4), writing on 28th August, 1871, says: "The Devonshire woody gall of the oak has appeared both here in Berwickshire and in Roxburgshire within the last year. It occurs also in various parts of Northumberland."

The appearance of the galls seems to have caused a panic; it was thought that they were produced at the expense of the acorn, and that pigs would lose their favourite food. Newspapers took up the cry with "Rally round the pig," "stand by the pig," and finally, when there seemed no chance of checking its spread, "Pity the poor pig." These fears proved to be groundless, though some damage may be done to young trees subjected to severe infestation.

In 1857 Frederick Smith (5) wished to satisfy himself as to the truth of the opinion then expressed that in the genus *Cynips* there is only one sex, namely female. In order to carry out his experiment he obtained from Devonshire a large supply of the galls of *C. lignicola* Hartig (*C. kollari*), "somewhere about a bushel and a half; every gall tenanted by the *Cynips* or its parasite, *Callimome devoniensis*." The *Cynips* emerged from the beginning of April, 1858, to the end of May, and he estimated that he had obtained not less than twelve thousand examples, and many hundreds of parasites. He examined all the *Cynips*, and all proved to be females. He placed sixty insects on low oaks in woods and hedges in different localities in the vicinity of London. In August he revisited the localities, and in about eight out of twelve found galls formed upon the very trees on which he had placed the *Cynips*, but none in their vicinity. From these galls he again obtained *Cynips* and placed them in isolated situations, and again found galls formed in about the same proportions as in the previous instance.

---

* The figures in parenthesis refer to the bibliography at the end of the paper.

Through the kindness of Mr. R. D. Eady of the British Museum (Natural History), who supplied me with insects, I was able to repeat the experiment. Insects were placed on buds on five dates between 5th May and 1st June, 1950, and kept under frequent but intermittent observation for 23 hours. At no time were they seen to insert their ovipositors, or indeed to show any interest in the buds. The buds produced spring growth ; no galls appeared.

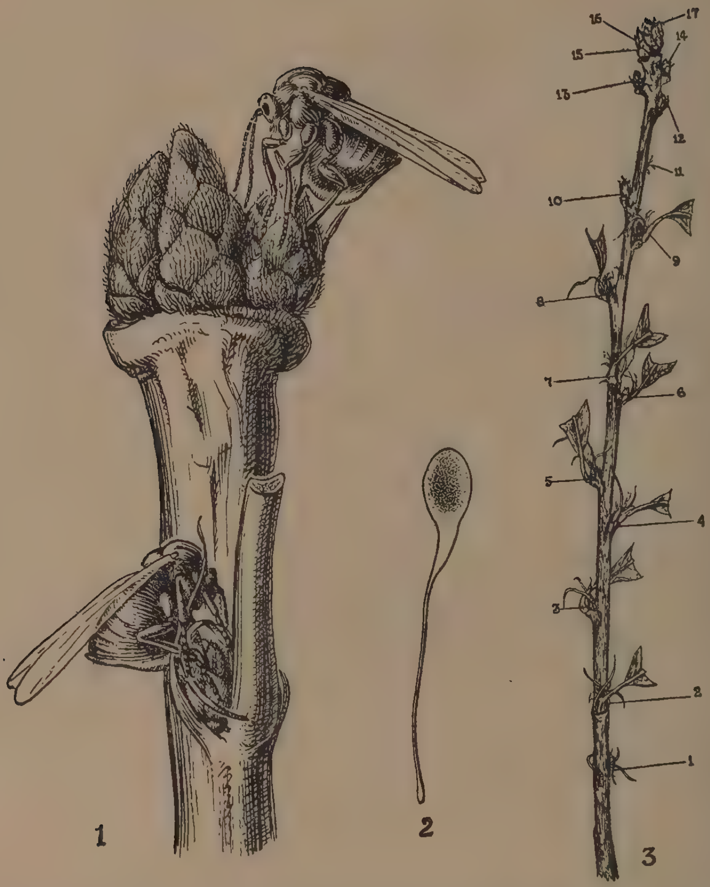
Beijerinck's (6) experiments with *A. kollari* are of great interest ; according to him *A. circulans* Mayr is its sexual generation. In 1898 he placed *A. kollari* on shoots of *Q. pedunculata* sleeved with gauze nets, but they showed no interest in the buds. He says, " the insects always ran towards the light, more repelled by all parts of the oak twigs than attracted to them." He then placed insects on shoots of *Q. cerris*, " and was immediately successful ; the insects quietened down at once ; they had obviously achieved their purpose in life. Shade or sun were now indifferent ; each wasp sought out a bud, stuck its laying-tube into it, and within an hour I had observed the laying of eggs." In these buds galls of *A. circulans* appeared in the following April, and on 12th May the first males and females emerged, " the legitimate children of the *kollari* mother." In the autunm of 1901 he repeated the experiment and again obtained the same result. Beijerinck failed in the second part of the experiment. He observed, " I have, however, not succeeded in getting *Andricus circulans* to lay eggs on *Q. pedunculata*, but I do not doubt that I shall achieve it this year or in one of the next few years." He saw *A. circulans* with its ovipositor inserted into buds of *Q. cerris*, which he says " may happen only in exceptional cases." It is curious that he never saw *A. circulans* copulating, although he brought hundreds of males and females together.

EXPERIMENTS WITH *Adleria kollari*.

Experiments were initiated in 1947 and continued till 1949 with the object of attempting to prove that Beijerinck was right in his assertion that *Andricus circulans* is the sexual generation of *Adleria kollari*. Trees of *Quercus cerris* Linn. and *Q. robur* Linn. were specially planted in my garden for use in the experiments and the shoots or branches on which insects were placed were sleeved, either with cellophane bags or talc cylinders. Greenwich mean time is given for all observations ; 24 hour clock system.

The insertion of the ovipositor.

The upper portion of a bud is selected and the ovipositor is extruded from the sheath ; the insect then probes to find a suitable point for insertion between the bud scales. After insertion the abdomen is gradually distended and a small portion in the region of the ovipositor becomes translucent. The tip of the sheath is raised to, or nearly to, the wings but there is some slight fluctuation as to position. The translucent portion is about 2 mm. long and



FIGS. 1–3.—(1) *Adleria kollari* inserting into buds of *Quercus cerris*. × 5. (2) Egg of *Adleria kollari*. × 60. (3) Shoot 12 of *Quercus cerris*. (Diagrammatic.)

1 mm. wide at the broadest part; with suitable lighting a pulsation can be observed taking place within. The time taken from the insertion of the ovipositor to the full distension of the abdomen is from 1¼ to 4 minutes. Fifty observations were made and the average time was 2.2 minutes. The position of the insect during the insertion of the ovipositor is either parallel with or at right angles to the bud, with its head pointing upwards unless it is at the extreme apex, when the head then points downwards (Plate I, fig. 1, and fig. 1).

Buds into which insects had inserted their ovipositors were examined and eggs were found embedded in the tissue. The egg is pyriform in shape, tapering off into a long peduncle (fig. 2).

Experiments carried out in 1947.

Insects placed in a Glass-topped Box with Cut Shoots of either Q. cerris, Q. robur *or both.*

The insects used in the following four experiments emerged on 10th September.

♀ and date.	Time.	*Quercus* sp.	Time in minutes per insertion in		First insertion	Notes.
			Terminal bud.	Lateral bud.		
A.	13.16–14.12	*cerris*	17	3, 7, 8, 8½	13.17	.
13/9	16.48–17.20	*robur*	.	.	.	Examined buds 6 times.
	17.23–17.49	*cerris*	.	7, 5, 7	17.32	.
		+ *robur*	.	.	.	.
B. 14/9	13.25–13.55	*robur*	7, 8	.	13.37	Insertion difficult owing to closely imbricated scales.
	17.38–19.00	,,	.	.	.	.
	19.02–19.38	*cerris*	22	7½	19.03½	.
16/9	10.00–11.10	*robur*	.	35½	10.06½	Bud dissected by B. W. H. Coulson and egg found embedded in leaf tissue.
	12.40–13.36	*cerris*	.	8, 9, 12	12.49	.
	13.37–14.02	*robur*	.	.	.	.
	14.03–14.59	*cerris*	.	16½, 15, 22	14.07	.
	15.00–16.00	*robur*	.	.	.	.
C. 14/9	09.35–09.50	*robur*	.	.	.	Did not stay on shoot although replaced 7 times.
	09.51–10.21	*cerris*	.	.	.	Moved off shoot 4 times.
17/9	12.50–12.57	*robur*	.	.	.	Ditto.
	12.58–13.37	*cerris*	5	.	12.59	3 minutes only on *robur*, no interest in buds.
		+ *robur*	.	.	.	.
D. 17/9	15.53–16.02	*robur*	.	.	.	Replaced on shoot 12 times.
	16.03–16.29	*cerris*	25	.	16.04	.
	16.30–16.45	*robur*	.	.	.	.
		+ *cerris*	11	.	16.34	.
	16.46–17.16	*robur*	.	.	.	.
		+ *cerris*	18½	.	16.57½	.

When a choice of host plant was given, the name of the species on which the ♀ was placed is given first.

Insects placed on living shoots of Q. cerris.

Insects were placed on 7 shoots between 20th and 25th September, two on each shoot. No detailed observations were made, but they were frequently inspected and seen with their ovipositors inserted into terminal and upper and lower lateral buds. Galls formed in the buds and a detailed account is given later in this paper.

Experiments carried out in 1948.

From the experiments carried out in 1947, when shoots of *Q. robur* were used, the interesting fact emerged that *A. kollari* is not always repelled, as stated by Beijerinck. Insects do at times insert their ovipositors into the buds and in one instance oviposition is known to have taken place. For this reason it was thought desirable to carry out four further experiments using living material in order to see, if insertion took place, what results, if any, would be obtained. The experiments were extended to obtain more data as to the reaction of insects switched over to shoots of *Q. cerris*.

Experiment (*i*).

♀ and date.	Time.	*Quercus* sp.	Insertions.	Removal.	Time.	Notes.
14 3/9	11.00	*robur*, branch 1	.	5/9	13.00	Observed 16 times; 1 lost in removal.
13 5/9	13.06	*cerris*, shoot 8	Very many, 1st at 13.07½, 1 insect	13/9	11.15	14.56, 11 inserting; maximum number 12 on 6/9 at 17.20. 56 observations made; on 3 only was no insertion seen. 1 insect died, 1 lost in removal.
11 13/9	11.35	*robur*, shoot 1	.	.	.	Observed till 12.05 and 6 times between 12.35 and 17.56.
11 14/9	.	Ditto	2 insertions	.	.	Observed 11 times; 1 insect died.
10 15/9	.	,,	3 ,,	.	.	Observed 13 times; 2 insects died.
8 16 and 17/9	.	,,	.	.	.	Observed 19 times.
8 18/9	.	,,	2 insertions	.	.	Observed 11 times; 7 insects died.
1 19–21/9	.	,,	.	.	.	Observed 29 times.
1 22/9	.	,,	.	.	.	Observed 5 times; insect dead at 17.43.

Experiment (*ii*).

♀ and date.	Time.	*Quercus* sp.	Insertions.	Re-moval.	Time.	Notes.
6 6/9	13.00	*robur*, branch 1	51 insertions	21/9	15.05	Observed 26 times; between 6–9 no insertion seen. Observed 134 times between 10–21. 1 insect lost in removal.
5 21/9	15.15	*cerris*, shoot 9	Very many, 1st at 15.16, one insect	.	.	Observed 7 times between 15.24 and 17.52 and 2, 3 or 4 were seen inserting.
5 22/9	.	Ditto	Very many	.	.	Observed 10 times; at 10.24 all 5 were inserting.
5 23/9	.	,,	Insertions	.	.	Observed 5 times; once no insertions.
5 24/9	.	,,	,,	.	.	Observed 10 times; on 7 no insertions. 2 insects died.
3 25/9	.	,,	.	.	.	Observed 6 times; 2 insects died. Remaining insect died 26/9.

Experiment (*iii*).

♀ and date.	Time.	*Quercus* sp.	Insertions.	Re-moval.	Time.	Notes.
5 11/9	13.55	*robur*, branch 2	1 insertion	16/9	10.44	Observed 43 times.
5 16/9	11.00	*cerris*, shoot 10	Very many, 1st at 11.01½	.	.	11.16, 3 inserting. Observed 13 times; on 1 only were no insertions seen.
17–26/9	.	Ditto	Many insertions	26/9	16.58	Observed 87 times; none inserting on 42. Deaths 1 on 21, 24 and 25.

Experiment (*iv*).

♀ and date.	Time.	*Quercus* sp.	Insertions.	Re-moval.	Time.	Notes.
5 16/9	12.45	*robur*, branch 3	7 insertions	24/9	13.05	Observed 93 times. On 22/9 an insect was seen 8 times inserting into the end of a piece of string used to tie the shoots together. It was examined by C. R. Metcalfe but no eggs were found.
5 24–28/9	13.11	*cerris*, shoot 11	Very many, 1st at 13.12; 1 insect	28/9	19.05	13.20, 4 inserting. Observed 45 times; on 6 only were no insertions seen. 2 insects dead at 18.00, 28/9.

Of the fifteen buds of *Q. robur* in which insertion took place, twelve dropped off, one produced a rosette of leaves and two spring growth. No galls appeared.

In October nearly all the buds on the shoots of *Q. cerris* used in the experiments fell off, as too many eggs had been laid in them. Some of these buds were sent to Dr. C. R. Metcalfe for examination. He reported as follows: "As you suspected, the buds are heavily infested, and in one case there were more than 50 eggs." Galls formed in some of the remaining buds.

The Incidence of A. kollari *Inserting into the Buds of a Small Tree of* Q. cerris.

Between 29th August and 14th September, 1948, ten insects were seen with their ovipositors inserted into buds. This is not surprising, as *Q. robur*, on which there were many marble galls, grew very close, and the branches of the two trees interlaced.

Experiments carried out in 1949.

These experiments were undertaken in order to obtain further data and to bring the *A. kollari* experiments into line with those carried out with *A. circulans*. Living shoot 12 of *Q. cerris* was used (fig. 3). Insects E and F emerged on 31st August and H on 4th September.

♀ and date.	Time.	Insertion into terminal or lateral bud.		Time in minutes.	Notes.
E.					
3/9	09.11–10.09	09.12–09.31	L.B.16	19	.
		09.32–09.46	L.B.16	14	Moved position on bud.
		09.46½–09.49	L.B.16	2½	.
		09.50–10.09	L.B.14	19	.
F.					
3/9	09.11–10.15½	09.12½–09.32	T.B.17	19½	Moved position slightly.
		09.32½–09.36	T.B.17	3½	Turned round twice on bud.
		09.37–09.46½	T.B.17	9½	Walked over insect E inserting into bud 16 without disturbing it.
		09.48–09.50	L.B.15	2	.
		09.51–10.02	T.B.17	11	.
		10.03½–10.15½	T.B.17	12	.
H.					
9/9	09.26½–11.28	09.27–09.41	L.B.4	14	.
		09.42–09.58	L.B.3	16	Moved position on bud.
		09.58½–10.05	L.B.3	6½	.
		10.05½–10.14	L.B.5	8½	.
		10.15	L.B.7	.	Abortive attempt to insert.
		10.16½–10.24	L.B.7	7½	.
		10.25	L.B.9	.	Abortive attempt to insert.
		10.27–10.36½	L.B.10	9½	.
		10.37–10.44½	L.B.12	7½	.
		10.45–10.50	L.B.13	5	.
		10.51–10.55	L.B.16	4	.
		10.55½–11.02	L.B.14	6½	.
		11.03–11.10	L.B.15	7	.
		11.11–11.17	L.B.11	6	Moved rapidly about stem.
		11.20	L.B.3	.	Abortive attempt to insert.
		11.22–11.28	L.B.8	6	Insertions were made into 12 out of 17 buds on the stem.

Four further experiments were carried out using insects G, I, J and K. I, J and K inserted freely, but G made three abortive attempts only and when placed on the shoot moved off at once. This insect was under observation for 50 minutes.

Observations made on Insect L :—

The insect was placed on cut shoots of *Q. cerris*, with one exception, when a shoot of *Q. robur* was used. Abortive attempts to insert ovipositor are not given.

♀ and date.	Time.	*Quercus* sp.			Insertions, time in minutes.	Notes.
13/9	12.42–13.16	*cerris*,	shoot	1	6½, 10, 4½, 3½	The observations lasted for 2 hours 22½ minutes; ovipositor inserted for 1 hour 36½ minutes.
	13.18–13.45	,,	,,	2	4½, 7, 10½	
	14.02½–14.31½	,,	,,	3	3, 6½, 7, 3	
	14.42–15.34	,,	,,	4	13, 3½, 6, 3, 8	
14/9	11.00–11.46	,,	,,	5	10, 2, 13½, 15½	The observations lasted for 1 hour 51 minutes; ovipositor inserted for 1 hour 32½ minutes.
	14.04–14.39	,,	,,	6	11, 14, 4	
	14.56–15.26	,,	,,	7	18, 4½	
15/9	12.47–13.09	,,	,,	8	3, 6½, 7	
	13.30–14.00	*robur*,	,,	8A		No interest shown in buds.
	14.08–14.49	*cerris*,	,,	9	14. 16½, 5, 3	
16/9	11.45–11.59	,,	,,	10	12	
17/9	11.29–11.38	,,	,,	10	3	
	13.35–13.58	,,	,,	10	2½, 5, 9½	
18/9	14.03–15.32	,,	,,	11	17½, 11, 16, 13, 23	
19/9	11.06–11.54	,,	,,	12	19½, 22	
20/9	20.51–22.28	,,	,,	13	5, 2, 2, 78	Observations made by electric light.

21*st September :* Insect placed on shoot 14 at 10.30. Between 10.30 and 11.03 no movement except for a slight tremor of the antennae. 11.03 movement of the wings, 11.07 lower wings spread out sideways and insect moved slightly, 11.09 wings again in normal position. 11.11 again a further slight movement of wings ; at 11.12 wings partly spread out, lower not attached to upper. Between 11.15 and 11.17 further slight movement of wings. 11.18 insect fell off shoot on to its back. Between 11.18 and 11.40 sporadic movement of wings, which were spread out from the body, and not joined ; the movement of the wings gave the body a rocking motion, but not enough to turn the insect over. No movement of the legs, which were drawn together ; at times some movement of antennae, abdomen slightly extended, tip of the ovipositor showing. At 11.40 the insect was turned over, but made no attempt to walk ; legs still drawn together, movement of wings continued ; 11.42–12.00 still spread out, some movement, observation ended.

Observed five times between 12.32 and 14.15, no movement, wings in normal position. 14.52, insect on its side, upper wings in normal position, lower slightly spread out. Observed seven times between 15.07 and 22.00, no change in position and no movement.

22*nd September :* 07.30, upper wings spread out, lower over abdomen. 11.15, upper and lower wings spread out, insect dead.

Insect L emerged on 8th September and was first placed on shoot 1 five days after emergence. It was on shoots, excluding those of *Q. robur* 8A and *Q. cerris* 14, for 9 hours 56 minutes, and during that time it inserted its ovipositor for 7 hours 55 minutes, the insertions lasting from 2 to 78 minutes. The insect lived for 14 days; the last insertion of the ovipositor was about 1½ days before death and within a few hours of becoming moribund.

ANDRICUS CIRCULANS MAYR.

INTRODUCTION AND OBSERVATIONS MADE IN 1948 AND 1949.

Early records.—The first record of the occurrence of *A. circulans* in Britain dates from the summer of 1876, when E. A. Ormerod (7) was given permission to search for galls on the trees in the Royal Botanic Gardens, Kew. She made careful and repeated search for galls on *Quercus cerris*, which she believed had hitherto been considered exempt from gall-growths in England. She found a very few specimens of a minute gall, some on a large tree labelled "*Q. cerris* var. *Lucombeana*," others on a large tree of considerable age labelled "*Q.*

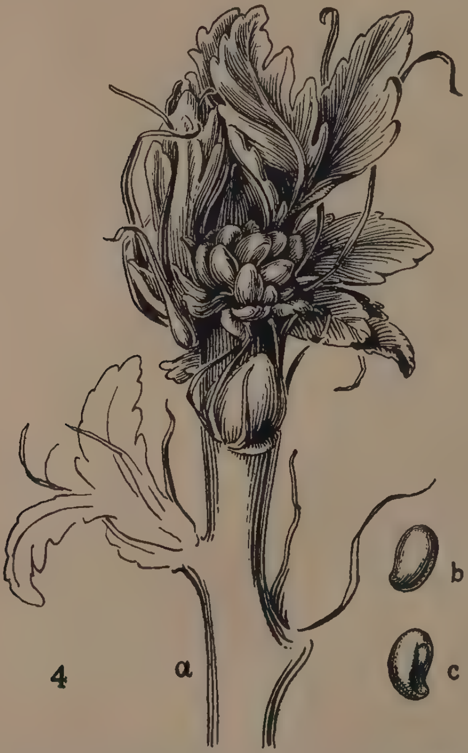


FIG. 4.—(*a*) Galls of *Andricus circulans*. × 3. (*b*) Gall ¾ dorsal view. × 3. (*c*) Gall ¾ ventral view. × 3.

cerris." The insects had emerged, and some of the galls were growths from the previous season. E. A. Fitch observes: "the above communication is especially interesting, as being the first authentic record of a Cerris gall occurring in Britain. Other Continental species will doubtless follow the introduction of their special pabulum, which is now so widely distributed in these islands, and when once established their march may be as rapid as has been that of *Kollari*."

Cameron (8) says, "Miss Ormerod found at Kew some galls which, although not quite typical, yet still may safely be referable to *A. circulans*."

Quercus cerris L. is a native of S. Europe and Asia Minor and was introduced into this country in 1735. Fitch's remark about its being so widely distributed in 1877 is of considerable significance.

Description of gall and time of appearance.—The galls appear in the terminal or lateral buds of *Q. cerris*, either singly or gregariously; I have noted up to nine (fig. 4 (*a*)). In shape they are oblong and when compacted together become compressed or flattened. They are glabrous, shiny and thin-walled, up to 3 mm. in length (fig. 4(*b*), and (*c*)). The colour of the galls I have seen has been Warm Buff or Warm Buff tinged with Eugenia Red.[1] They appear between the bud scales in April.

Emergence of insects.—The insects emerge in April, May and the early part of June and have a more regular time of emergence than is the case with *A. kollari*, the usual time being the early morning. Galls were examined between 24.00 and 01.00 on 15th May, 1949, and insects were seen enlarging exit holes. Emergence takes place from an exit hole about 1 mm. from the apex (fig. 5(*a*) and (*b*)).

The appearance in 1948 *of galls produced under control.*—The 7 shoots of *Q. cerris* on which *A. kollari* were placed in the autumn of 1947 were closely watched during March. Towards the end of the month many of the buds on nearly all the shoots were destroyed by tits. To prevent further damage the shoots were cut and placed in water under cover. At that time no galls were visible, but very early in April they appeared. Only two shoots had completely escaped damage by the birds, 2 and 7. On shoot 2 there were 6 galls and on shoot 7, 16 galls, 7 in the terminal bud and 5, 3 and 1 in lateral buds.

Emergence of insects from galls produced under control.—On 14th April the first insect emerged, a male. Emergence continued up to the 23rd. The total number of insects obtained was 23, of which 5 were males. Between the 19th and 23rd 12 insects emerged, all females. All the insects emerged in the early morning. From several galls there was no emergence.

The first appearance of galls in 1949.—On 10th April 2 galls, which were later destroyed by birds, were observed on the tree of *Q. cerris*; on the 16th, 3 more, and on the 22nd several. Some of these were produced under control. Many

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[1] The colour terms used for galls throughout the paper are taken from Ridgway, 1912, *Color Standards and Color Nomenclature*, Washington.

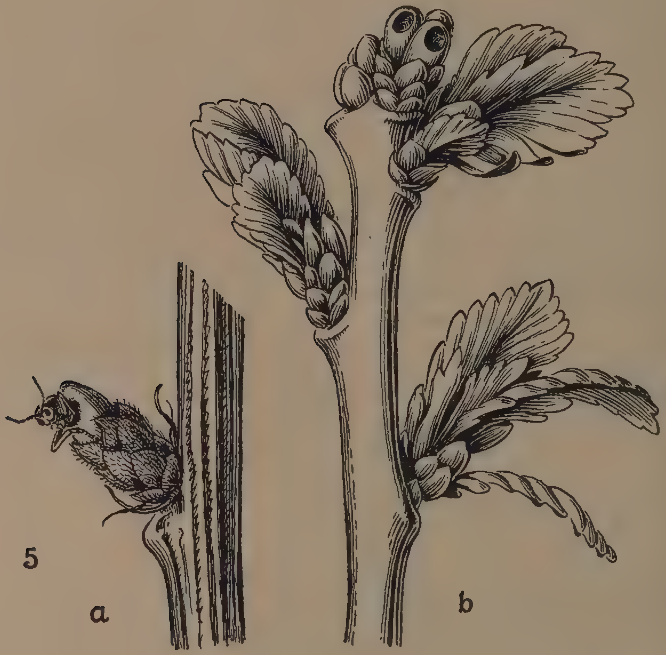


FIG. 5.—(*a*) *Andricus circulans* emerging. × 5. (*b*) Galls showing exit holes. × 3.

galls were also collected from other trees in the vicinity and placed in glass-topped boxes for observation.

Emergence of insects.—Emergence commenced on 27th April and continued till 3rd June, when the last insect appeared, a female. Between these dates 123 insects emerged, 44 males and 79 females. Of these 32 males and 64 females emerged in the early morning, and 12 males and 15 females during the day. The galls were examined twice a day, usually between 08.00 and 09.00 and 19.30 and 22.00.

In captivity the average length of life of the male is 2.7 days and that of the female 4.8 days. These data are based on observations made on 16 insects of each sex.

Emergence of parasites.—Between 28th May and 19th June a considerable number of Chalcid parasites emerged from the galls; the material was sent to Mr. J. F. Perkins for determination. Three species were determined, *Amblymerus erichsoni* Rtz., (det. C. Ferrière), 35 males and 31 females; *A. xanthocerus* Ths., 6 males and 5 females; and *A. tibialis* West., 1 male. Of *A. xanthocerus* he says, "another host for this is stated to be *Bioryhza pallida* Oliv., it was described from specimens bred from that host."

EXPERIMENTS WITH *A. circulans.*

The insertion of ovipositor.

The ovipositor is inserted into the lower portion of a bud, and the insect carries out the operation with its head pointing downwards (Plate I, fig. 2), in these points differing from *A. kollari.*

Two buds of *Q. robur,* into which a mated insect was seen to insert its ovipositor, were examined and an egg was found in each, embedded between the leaf tissue, one more deeply than the other.

The egg is narrowly obovoid-ellipsoid, tapering off into a long peduncle (fig. 6), thus differing greatly in shape from that of *A. kollari.*

Experiments carried out in 1948.

The insects used in the experiments were those that emerged from galls produced under control, They were placed on sterile shoots of a small tree of *Q. robur* grown in a pot. The work was much handicapped owing to the small proportion of males, 5 only, the last of which died on 19th April, and to the fact that the bud scales were too closely imbricated to allow easy insertion of the ovipositor.

On 18th April at 11.50 1 male and 2 females were placed on a shoot, mating had been observed earlier and again took place when the insects were on the bag. The insects were observed many times, but showed no interest in the buds; most of the time was spent on the bag.

On the 18th 1 male and 3 females were placed together; while under observation no mating was seen.

On the 19th at 13.00 the 3 females were placed on a second shoot. The observation lasted till 14.10; on three occasions one insect made three abortive attempts to insert its ovipositor. When observed between 14.30 and 15.00 there was no attempt to insert, but some interest was shown in the buds. When observed on several other occasions, no attempt was made to insert.

On the 20th at 10.05 the 3 females were placed on a third shoot. The observation lasted till 11.05, but no interest was shown in the buds. When again observed between 11.20 and 13.00, and on several other occasions, no interest was shown in the buds.

On the 22nd 4 virgin females were placed on a fourth shoot, and observed many times; they moved about the stem and buds but made no attempt to insert.

The Incidence of A. circulans *Inserting in the Buds of a Small Tree of* Q. robur.

On 27th April at 11.40 *A. circulans* was seen with its ovipositor inserted into a bud of *Q. robur.* The shoot was sleeved to prevent the insect escaping; it moved off the bud shortly after, and, up to 12.00, made no further attempt to insert, though it moved about the buds. At 13.00 it was on the bag and was removed. At 13.15 it was placed on a fourth shoot of the small tree in the pot; the observation lasted till 14.15. It spent most of its time on the bag and showed no interest in the buds. It was observed on several occasions on the 27th and 28th but no interest was shown in the buds.

The bud on which the insect was first observed was marked; it produced spring growth, and in June a gall appeared in a lateral bud. The inference is that the insect seen with its ovipositor inserted was responsible for the gall, though this assumption cannot be accepted as a proved fact unsupported by evidence obtained under the strictest experimental conditions, using sleeved sterile shoots. If under these conditions galls can be produced, the assumption can then be accepted as proved.

OBSERVATIONS MADE IN 1949.

Mating.

A series of observations were made on the behaviour of males and females when placed together, but it was not always possible to follow their movements. Males and females were separated when the boxes containing the galls were examined night and morning, but in some cases mating had probably taken place.

A male that emerged on 28th April and a female that emerged on 2nd May were placed together at 13.07 on the 2nd. The male was in a partly moribund condition but able to move about slowly. It showed no interest in the female. At 14.17 the insects were brought into contact and mating took place at once lasting for 30 seconds ; a second mating took place at 14.19 for 7 seconds and a third at 14.20 for 13 seconds. The observation ended at 14.30 ; at 15.15 the male was dead.

The female was placed on a cut shoot of *Q. cerris* at 14.30. It moved off without showing any interest in the buds, but at 15.00 a bud was selected and it inserted its ovipositor.

A male that emerged on 3rd May and a female that emerged on the 2nd were placed together at 08.48 on the 5th. At 09.00 mating took place lasting for 60 seconds ; a second mating took place at 09.05 lasting for 30 seconds. Except for these two matings the male showed no interest in the female, though they often passed close to each other and even met head on. The observation ended at 10.10. Both insects died on the 6th.

A male that emerged on 5th May and a female that emerged on the 3rd were placed together at 10.40 on the 5th. At 11.02 the male showed some interest in the female, but made no attempt to mate ; at 11.05 mating took place lasting for 40 seconds, at 11.17 the male again showed interest in the female but did not mate. No further interest was shown up to 11.45, when the observation ended.

A male and female that emerged on 12th May were placed together at 09.49 on the 12th. At 10.02 mating took place, lasting for 38 seconds. Connection was seen ; the observation ended at 10.05.

A second pair that emerged on the 12th were placed together at 10.19. At 10.20 mating took place lasting for 39 seconds ; connection was seen. The antennae of the male were much agitated at the beginning of the mating, then still. Two abortive attempts to mate were made at 10.30 and 10.42 ; the observation ended at 10.50.

A third pair that emerged on the 12th were placed together at 09.14 on the 13th, mated at once for 45 seconds. Connection was seen ; the observation ended at 09.30.

A fourth pair that emerged on the 12th were placed together at 09.40 on the 13th. At 09.45 mating took place, lasting for 24 seconds ; abortive attempts were made at 09.48, 09.49 and 09.49½, but the female kept moving. At 09.54 a second mating took place lasting for 24 seconds; connection was seen. There were further matings at 09.55 for 16 seconds, 09.56 for 20 seconds and at 09.58½ for 38 seconds. At 10.01 interest was shown and at 10.06 there was another mating lasting for 18 seconds; during this the female moved about. The observation ended at 10.10.

A fifth pair that emerged on the 12th were placed together at 10.14 on the 13th. At 10.15 mating took place lasting for 84 seconds; connection was seen. The antennae of the male were much agitated; the observation ended at 10.30.

A male and female that emerged on 24th May were placed together at 21.25 on the 25th, the observation being made by electric light. The male showed no interest in the female, and at 21.36 was placed with another female that also emerged on the 24th. At 21.40 mating took place lasting for 51 seconds, connection being for 42 seconds. Mating again took place at 21.55 for 6 seconds and at 21.56 for 4 seconds. There was a further mating at 21.59 for 16 seconds, connection being for 8 seconds. No further interest was shown in the female up to 22.06, when the observation ended.

From the above observations it will be seen that mating takes place very rapidly, and that the same male and female may mate several times. When connection was definitely seen the fact was noted, but sometimes, owing to the position of the insects, it was not possible to be certain on this point.

The Incidence of A. circulans *on Scrub Oak, on Shoots from an Oak Stool, or on a Small Tree of* Q. robur *in* 1949.

May 1st: Observation on scrub oak from 13.00 to 13.30. One seen with ovipositor inserted into a bud.

May 13th: Two observed on *Q. robur* one moving about a shoot, the other with its ovipositor inserted into a bud from which there was spring growth; a gall formed in a lateral bud on this shoot.

May 16th*:* Two observed moving about shoots.

May 17th: Two observed, one moving about a shoot, the other moved across a cellophane bag.

May 21st: Observation on shoots from oak stool from 14.30 to 15.20, sunny, wind light, S.W. Several insects were seen and seven caught; five had their ovipositors inserted into buds. One shoot with five buds had insects inserting into three of them at the same time. The shoot was cut and placed in a tube without disturbing them.

May 22nd: Observation on shoots from oak stool from 13.25 to 14.05, no sun, wind rather strong, S.W. Seven insects were seen with their ovipositors inserted into buds, and twelve more were noted moving about the buds and stems. At 13.35 one was seen examining a bud; it made an abortive attempt to insert its ovipositor, then moved away, returned to the bud at 13.37 and made another abortive attempt at 13.37½; again moved away and down the shoot at 13.40.

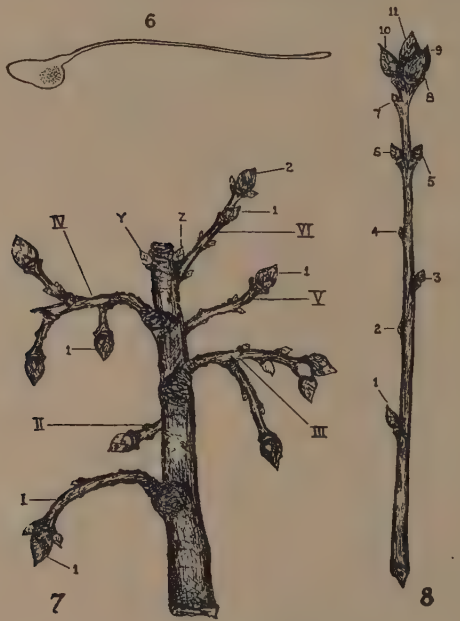
May 30th: Observation on shoots from oak stool from 15.05 to 15.25, sunny, wind strong, S.W. No *A. circulans* seen, but many small Hymenopterous insects were moving about the stems and leaves.

June 4th: Observation on shoots from oak stool from 15.00 to 15.20, sunny, wind strong and cold, N.W. No *A. circulans* seen, but many small Hymenopterous insects were again seen moving about the stems and leaves.

Within 240 yards, to the west of the oak stool, there were two large trees of *Q. cerris* on which galls of *A. circulans* were abundant; many marble galls formed in the buds on the spring growth from the oak stool in 1949.

Experiments carried out in 1949.

The experiments were carried out under the strictest control conditions. Shoots and branches on a tree of *Q. robur* were selected and sleeved before *A. circulans* started to emerge, so that sterile material would be available on which to place insects. The insects used were either those that emerged from collected galls and mated in captivity, or "wild" insects, one caught with its ovipositor inserted into a bud, the other three moving about shoots.



Figs. 6–8.—(6) Egg of *Andricus circulans*. × 60. (7) Branch 4 of *Quercus robur*. (Diagrammatic.) (8) Shoot 3 of *Quercus robur*. (Diagrammatic.)

Experiment 1.

The insect used in this experiment was mated under control on 28th April and placed on branch 4 of *Q. robur* (fig. 7) at 11.55.

The following observations were made: 28*th April:* 12.40, sitting on bud 1 shoot I; 12.45 moved off on to cylinder. 13.30, on cylinder. 15.50 ovipositor inserted into bud Z. 16.20, ovipositor inserted into bud Z when observation started, withdrawn 16.45, moved off bud. 16.45 to 17.00, examined various buds and moved about stems and cylinder. 17.00 abortive attempt made to insert ovipositor into bud 2 shoot VI, moved off and down stem and up to bud Y. 17.03, ovipositor inserted, withdrawn 17.47. 17.49 moved away and down the stem, then returned to bud Y, when an abortive attempt was made to insert ovipositor at 17.50 ; 17.52, moved off bud, returned 17.54, when another abortive attempt was made at 17.55. Off bud and moved about stems, back to bud Y, ovipositor inserted at 18.00. Observation ended.

29th April: 08.20, ovipositor inserted into bud 1 shoot I ; withdrawn 08.23. 08.23 to 08.50 moved about the stems and examined buds. 08.51 ovipositor inserted into bud 1 shoot IV ; withdrawn 08.54 ; flew off bud. 09.25 ovipositor inserted into bud 1 shoot V, withdrawn 09.59, moved to bud 2 shoot VI ; 10.01 ovipositor inserted, withdrawn 10.55, slight change in position ; ovipositor inserted again 10.56 withdrawn 11.32. The insect then moved to the opposite side of the bud ; ovipositor inserted 11.33. When the observation ended at 12.05 the ovipositor was still inserted. 12.25, ovipositor inserted into bud Z. 14.55, ovipositor inserted into bud 1 shoot V, withdrawn 15.03, moved to bud Z, 15.04, abortive attempt, moved off 15.05 and to bud 2 shoot VI, 15.06 ; ovipositor inserted 15.07, withdrawn 15.11, then moved to the opposite side of bud, ovipositor inserted 15.12, withdrawn 15.47. Moved to bud Z, 15.48, abortive attempt, off at once, observation ended. 16.12, moving about stems ; 16.13, abortive attempt to insert ovipositor into bud 2 shoot VI ; 16.15, flew off on to cylinder. 17.10, on cylinder ; 17.12, back on to stem ; 17.13 examining buds, back on to stem moving about rapidly, then to bud 2 shoot VI, ovipositor inserted 17.19, withdrawn 18.00, moved off bud. Between 18.00 and 18.07 the insect moved to bud Z twice, then to bud 1 shoot VI ; no attempt was made to insert ovipositor. At 18.07½ it again moved to bud Z ; 18.08, ovipositor inserted, withdrawn 18.20 when the observation ended and the insect was removed.

Notes.—The insect was placed on the branch at 11.55 on 28th April and removed at 18.20 on the 29th. During that time 6 hours 57 minutes were spent observing its movements. It was seen inserting its ovipositor into six buds, into two for very short periods ; bud 2 shoot VI was the most frequented. The length of time the ovipositor was inserted was 5 hours 31 minutes, the insertions varying from 3 to 54 minutes.

Buds Y and Z produced spring growth, the others rosettes of leaves only.

Bud 2 shoot VI was unfortunately broken off in removing the tiffany bag which was substituted for the cylinder. All branches or shoots used in controlled experiments had to remain covered for a considerable period till all risk of uncontrolled insects visiting the buds had passed.

On 8th June a gall appeared in the terminal bud of the spring growth from bud Y. As it had been badly attacked at an early stage by the inquiline *Synergus reinhardi* Mayr, growth was arrested when it was only 9 mm. long by 8 mm. broad. Three galls appeared on the spring growth from bud Z, one in the terminal bud and two in upper laterals. The gall in the terminal bud appeared on 10th June. The date of the appearance of the other two was not noted, but on 10th June one was 5·5 mm. long by 3 mm. broad, the other 2·2 mm. long by 1·9 mm. broad. The growth of these two galls was very unequal ; the final measurement for one was 20 mm. long by 23 mm. broad and for the other 12 mm. long by 13 mm. broad. Until about the middle of

August it seemed as if the gall in the terminal bud was aborted, but it then started to increase in size. On 12th September it was 1.1 mm. long by 1.3 mm. broad, and reached its maximum of 16 mm. long by 17 mm. broad by 24th September. It was still Lime Green in colour on 16th October.

No *A. kollari* emerged from any of the galls.

Experiment 2.

The insect used in the following experiment was caught on 1st May with its ovipositor inserted into a bud on a scrub oak. On 2nd May at 09.18 it was placed on shoot III of *Q. robur* (fig. 8). The following observations were made: 09.19½ moved from bag on to shoot and to bud 8; 09.20 abortive attempt to insert ovipositor; 09.22 moved off; 09.22–09.24½ moved about upper buds; 09.25 abortive attempts to insert into bud 10; 09.26 moved to bud 8, abortive attempt to insert ovipositor; 09.27 ovipositor inserted; 09.42½ withdrawn, moved to another position on same bud, 09.43 ovipositor inserted; 09.49 withdrawn; moved about the bud, 09.50½ ovipositor inserted in a new position; 10.08 withdrawn, again moved position slightly; 10.08½ ovipositor inserted; 10.11 withdrawn; moved position, 10.11½ ovipositor inserted, 10.26 withdrawn.

Two abortive attempts were made to insert at 10.26½ and 10.27. Moved to bud 11; 10.28 ovipositor inserted, 10.47 withdrawn; moved position and an abortive attempt made at 10.47½. 10.48 moved to bud 9; 10.49 ovipositor inserted, 11.07 withdrawn, moved position slightly on bud; 11.07½ ovipositor inserted, 11.21 withdrawn, again moved position; 11.22 ovipositor inserted, 11.30 withdrawn, moved off on to stem. The insect was then removed and the observation ended.

Notes.—The observation lasted for 2 hours 12 minutes, and during that time the insect had its ovipositor inserted for 1 hour 54½ minutes. Bud 8 was most frequented; the insect inserted its ovipositor five times varying in length from 2½ to 17½ minutes; into bud 9 the ovipositor was inserted three times varying in length from 8 to 18 minutes, and into bud 11 once for 19 minutes. On 28th May a gall appeared in a lateral bud on spring growth from bud 8, and on 30th May one appeared in a lateral bud on spring growth from bud 9. No gall formed on the spring growth from bud 11.

The Development of the Marble Gall that appeared on the Spring Growth from Bud 8 *on Shoot* 3.

28th *May:* A gall enclosed in an Ox-blood Red epidermis was observed as a very small growth between the scales of a lateral bud (Plate II, fig. 1).

7*th June:* The bud scales had fallen off. Gall ovoid, 3mm. long by 2·25 mm. broad. Except at the base, which was still Ox-blood Red, the epidermis had darkened to Maroon. It was densely clothed with minute white erect bristle-like hairs (Plate II, fig. 2).

12*th June:* Gall broadly ovoid, 4·6 mm. long by 3·2 mm. broad, epidermis Maroon (Plate II, fig. 3).

17*th June:* Gall sub-spherical, 6 mm. long by 5·5 mm. broad. Owing to the swelling of the gall the epidermis had ruptured and broken up into numerous small scales of unequal size, irregularly dispersed over its surface. At the apex the epidermis was still unbroken and rose to a point, the so-called "stigma." Gall Grape Green and scales Maroon. The minute bristle-like hairs still retained.

20th June: Gall sub-spherical, 8·5 mm. long by 7·5 mm. broad, Grape Green. Further disintegration of the epidermis had taken place round the apex, but the pointed portion was still intact, (Plate II, fig. 4).

27th June: Gall spherical, 13 mm. long by 14 mm. broad. Light Cress Green with areas of Grape Green. A few small scattered scales still remained, more numerous and larger at the apex, where there was still a very small unbroken portion of epidermis rising to a blunt point, Maroon (Plate II, fig. 5).

4th July: Gall 17 mm. long by 18 mm. broad, maximum growth. The raised portion of the epidermis at the apex had now flattened and become an irregular shaped scale, Liver Brown in colour. Gall Light Cress Green with small areas of Grape Green.

11th July: Gall now almost completely Light Cress Green.

21st July: Colour Jade Green with areas of Light Cress Green. There were still a very few minute scale fragments adhering to the gall, Liver Brown in colour. Cinnamon-Brown scars in the apical region; also scars of the same colour on the body of the gall, and some small speckles of Ochraceous-Buff, sometimes with very small scale fragments in their centres. These speckles mark the places where scale fragments had adhered, so inhibiting the development of the green.

31st July: Gall starting to mature, the green colour had become dull—the first phase of the transition stage.

8th August: Gall mostly Light Yellowish Olive with dull Jade Green still showing; there are also areas of Isabella Colour.

15th August: Gall now mostly Verona Brown, but still a very slight trace of Light Yellowish Olive. The Isabella Colour areas were darkening to Tawny-Olive.

22nd August: Final colour of the gall Verona Brown with areas of Tawny-Olive, (Plate II, fig. 6).

Notes.—There was no emergence of *A. kollari* from this gall, or from the one on the spring growth from bud 9, which when fully developed was 17 mm. long by 19 mm. broad.

Eight further experiments were carried out using branch 5 and shoots 2, 4, 6, 7, 8, 9 and 10. Many hours were spent observing and insertion was seen in all cases.

One gall only appeared, in a lateral bud on the spring growth on shoot 6; it became aborted. The insect that inserted was mated under control.

Observations on the Behaviour of a Virgin Female when placed on Buds.

On 29th May a shoot of *Q. robur*, from which all the buds but one had been removed, was placed in a glass-topped box and a virgin female introduced on to the partly expanded bud at 11.20. While under observation till 11.57, during which time it moved off the bud and was replaced a considerable number of times, it made eight abortive attempts to insert its ovipositor.

Another shoot was then used with the bud less expanded. The following observations were made: Insect on glass lid 12.00. 12.40 ovipositor inserted into bud. 13.02, moving about bud; 13.03 ovipositor inserted, 13.29 withdrawn. Abortive attempts to insert ovipositor at 13.30 and $13.32\frac{1}{2}$, 13.33 ovipositor inserted, 13.54 withdrawn. 14.40 ovipositor inserted, 14.49 withdrawn. Observed seven times between 15.15 and 18.30; no further insertions seen.

On 2nd June Dr. C. R. Metcalfe dissected the bud and found an egg between the foliage leaves in the outer part. The peduncle was very firmly attached to the leaf tissue, and when the egg was removed from the bud some of the tissue remained attached to it. Further investigation was made and a second egg was found more deeply embedded, also very firmly attached to the leaf tissue by the tip of the peduncle.

The experiment proves that, given buds in the right condition, an unmated female will insert her ovipositor and investigation of the bud shows that oviposition actually takes place.

The Incidence of Inquilines and Parasites Inserting their Ovipositors into, or Emerging from Galls produced under Control.

The galls suffered constant attacks from inquilines and parasites from the latter part of June to the early part of October. The following were observed and caught, either with their ovipositors inserted or examining galls. The material was submitted to Mr. R. B. Benson for determination.

June: The inquilines *S. reinhardi* and *S. umbraculus* Ol. were very frequent during the latter part of the month; they persistently inserted their ovipositors into the galls. The gall on the spring growth from bud Y on branch 3 was attacked in a very early stage when it was only 4·5 mm. long by 3 mm. broad, and before the epidermis had scaled off. When inserting its ovipositor the insect assumes a position with its head pointing downwards (Plate I, fig. 3).

Insects seen with ovipositors inserted into galls.	Insects seen examining galls.
July: *Torymus regius* Nees, *Synergus umbraculus* Ol., *Eurytoma rosae* Nees, *Megastigmus dorsalis* F.	*P. simplex.*
August: *T. regius, E. rosae, M. dorsalis, Eupelmus urozonus* Dal.	*S. umbraculus,*
September: *T. regius, E. urozonus.*	
October: *Platyterma simplex* Thoms.	

On 14th August a small exit hole was noted in the largest gall on the spring growth from bud Z on branch 3, and on the same day an insect was seen emerging from another hole. On the 16th another exit hole was seen near the apex of the gall with an insect on the point of emerging. The gall was not then mature, but in the transition stage, Lime Green with small areas of Light Cress Green but mostly Yellowish Olive, with areas of Isabella Colour. The three exit holes were in the Isabella Colour area.

On the 17th at 11.30 the head of an insect was seen in the opening of the exit hole near the apex. The gall was sleeved and observations made at intervals. The insect emerged between 15.30 and 16.25 after the hole had been further enlarged. On the 21st there were six exit holes, and at 11.45 there were indications in the shape of rings of "sawdust" that further emergences would take place from two of them. At 14.06 one insect emerged, and at 14.06½ the other started, thorax and first pair of legs out, the second pair out and wings partly out at 14.08, and shortly after the whole insect emerged, and at 14.09½ was moving about the gall. Five insects were caught and identified as *S. umbraculus*. It is of interest to note that in three cases two insects emerged from the same exit hole, so that nine insects emerged from six holes. On 8th September a female *Torymus regius* Nees emerged from the gall. The first date on which *T. regius* was observed with its ovipositor inserted into the gall was 14th July.

At the end of November there were fifteen exit holes in the gall, and one in the small gall on the same shoot.

Emergence of parasites and inquilines in 1950.

The following parasites and inquilines emerged from the galls produced under control during the spring and early summer of 1950 :—

	S. reinhardi.	*S. umbraculus.*	*T. regius.*	*Eurytoma* sp.
March . .	.	.	.	1♀
April . .	9♂	1♂	.	.
May . . .	6♂, 16♀	17♂, 3♀	1♂, 3♀	.
Totals .	15♂, 16♀	18♂, 3♀	1♂, 3♀	1♀

General Description of the Marble Gall.

The gall, enclosed in an epidermis, first appears as a very small growth between the bud scales of axillary or terminal buds on spring growth. At first the gall is ovoid and appears in the centre of the bud, or it may break through the side. The colour of the epidermis may be Ox-blood Red, Nopal Red or green tinged with Ox-blood Red. The bud scales fall off at an early stage and the epidermis darkens to Maroon ; the apical point may remain Ox-blood Red for a longer or shorter period. The epidermis is either densely clothed with minute white bristle-like hairs, sometimes with a few longer ones intermixed, or there may be only a few hairs. As the gall develops the lower portion of the epidermis is ruptured into small scales, the rupturing process spreading upwards till only a very small portion round the apex remains unbroken. The scales darken in colour to Liver Brown. The pointed portion of epidermis at the apex often persists, and is very pronounced when the growth of the gall has been arrested at an early stage.

The colour of the immature gall varies greatly ; and may be Cress Green, Light Cress Green, Lime Green or Jade Green ; there are also colour combinations—Light Cress Green and Grape Green, Light Cress Green and Jade Green, Lime Green and Cress Green, Lime Green and Light Cress Green, Lime Green and Jade Green, Old Gold and Light Cress Green, Old Gold and Lime Green, and Old Gold and Jade Green. It is probable that other colours and colour combinations also occur. A gall on shoots containing much anthocyanin may have larger or smaller portions flushed or coloured Deep Liver Brown or Ochre Red. The surface of the gall is glabrous and may be shiny or matt. There are a larger or smaller number of small Ochraceous-Buff speckles on the galls marking the places where fragments of scale had adhered, so inhibiting the development of the green ; there may also be Cinnamon-Brown scars, especially in the apical region.

Just before the gall reaches maturity the colour passes through a transition stage, the original colour becoming dull, and giving place to Light Yellowish Olive, which in turn changes to some shade of brown.

The colour of the mature gall also varies greatly and may be Olive-Brown, Verona Brown, Isabella Colour or Cream-Buff ; there are also colour combinations :—Verona Brown and Isabella Colour, Sayal Brown and Isabella Colour, Russet and Isabella Colour, Olive-Brown and Buffy Brown, Buckthorn Brown and Cream-Buff, and Chamois and Cream-Buff. The colours were determined as soon as the galls were mature ; other colours and colour combinations no doubt occur.

A normally developed gall is spherical and may be smooth or have protuberances on its surface—the " papillae " of Connold. There is a very considerable range in size. The largest I have seen, after examining many hundreds was 25 mm. long by 25 mm. in diameter ; the smallest, from which *A. kollari* had emerged in the first year, 14 mm. long by 14 mm. in diameter. M. Niblett (9) has found very few large galls, several 27 mm. and 28 mm. in diameter being the largest. From two galls 10 mm. in diameter he had emerge in the second year two perfectly formed but considerably undersized *kollari.* Many galls become aborted at an early stage owing to the death of the larva, which may be caused by the intrusion into the larval chamber of inquiline larvae.

The galls appear either singly, two or three together or in clusters, and at times two, more rarely three, may be fused together. Galls are to be found frequently in great profusion on the spring shoots produced by young trees, scrub oak or oak stools. Few, if any, are to be found on mature trees as they produce comparatively little spring growth.

Emergence of Insects and Completion of Life-cycle.

The insect normally emerges in August and September of the year in which the gall is formed, but may overwinter and emerge in June, July and August of the following year. Observations were made on the emergence of insects in 1948 and 1949. Emergence from 1948 galls commenced on 21st August and ended on 27th September, and from those collected in 1947, not a great number, from 17th to 31st July. Emergence from the 1949 galls commenced on 24th August and ended on 17th September, and from those collected in 1948 it extended from 29th June to 30th August. Niblett (10) has had emergences in " July, August, September and October of first, or June, July, August and September of the second year, the majority taking place in August and September of both years." There is no particular time during the day when emergence takes place.

In September, 1948, a series of five observations were made on the actual emergence from the gall and on the period shortly before when the enlarging of the exit hole was being completed. The length of time taken by an insect to reach the surface is not known ; several sections were cut, and in some cases insects were seen tunnelling their way out. The first indication that an insect is about to emerge is the appearance of a hole about the size of a pin-point in the wall of the gall. In one of the observations such a hole was seen on 8th September at 18.30 and the insect emerged on the 9th at 10.36½. The other four observations started when the exit hole had already been considerably enlarged, so there are no data as to the length of time that elapsed between the first appearance of the hole and emergence. The pattern followed by the insects in biting their way out, and their behaviour on emergence, was very uniform. The exit hole was gradually enlarged by the insect biting away the outer wall of the gall, the head was raised above the opening and the " saw-dust "was deposited round the edge. There were periods of biting and periods of rest, and the head and antennae were at times withdrawn below the opening. During the enlarging operation the insect moved its whole body round in the tunnel and so was able to cut a circular hole. Before emergence was attempted great care was taken to smooth off all rough edges ; in each case the hole was enlarged to the right size to allow the insect to emerge at the first attempt. Emergence was fairly rapid, lasting from 1 to 2 minutes, and was carried out in three stages. First the thorax and first pair of legs appeared above the hole (fig. 9(*a*)), followed after a short pause by the second pair of legs, and after a further pause the insect heaved itself out, using the first pair of legs for leverage (fig. 9(*b*)). At once, or almost at once, the insect moved off the gall and on to paper on which the gall had been placed. All parts of the body were very thoroughly and repeatedly cleaned, and several times the wings were pressed under the abdomen by the third pair of legs during the cleaning process, which started within 30 seconds of emergence. There was at times considerable, sometimes very rapid movement on the paper. Putty-coloured excrement was voided during movement within 1 to 2 minutes of emergence. Within 8 to 16½ minutes of emergence the " ovipositing " position was assumed and the ovipositor was withdrawn from the sheath. In one instance it was rotated in a curious way. The wings were vibrated several times, and

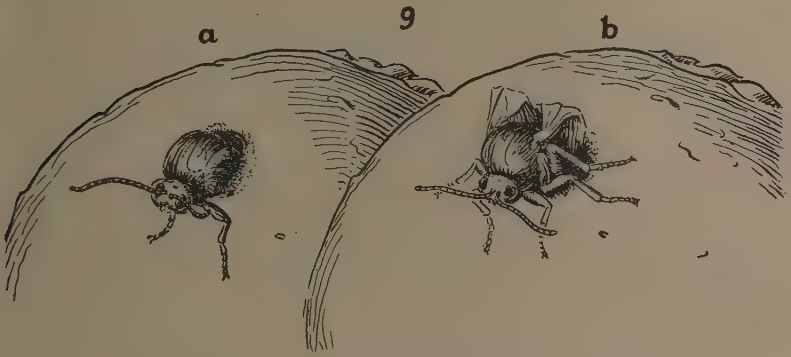


Fig. 9.—(*a*), (*b*) Emergence of *Adleria kollari*. × 5.

sometimes very short flights were made before the insect finally flew strongly away 22 to 37½ minutes after emergence.

The time spent making the observations to obtain these data was 5 hours 34 minutes. Some further observations were made to ascertain if the exit holes were always enlarged to the right size to allow the insects to emerge at the first attempt. In one of these a pin-point hole was seen on 10th September at 21.15 and the insect emerged on the 11th at 09.20. Only one case was noted in which the hole was not large enough and the insect became wedged when only the thorax was out; it withdrew and further enlarging of the hole took place. A second attempt failed, though this time the front legs also appeared; it again withdrew and the hole was still further enlarged. At the third attempt it forced itself out after a struggle; both first and third legs were used as leverage to force out the abdomen.

The diameter of the exit hole is from 1·5 to 2·5 mm., but 2 mm. is the most usual.

In captivity the average length of life is 13·2 days. These data are based on observations made on 24 insects.

SUMMARY.

The Marble Gall was first observed in Devonshire about 1830. Within 40 years the galls had spread to, at least, two of the southern counties of Scotland.

During the autumns of 1947–49 detailed observations were made on *A. kollari*. In 1947–48 change-over experiments were carried out, in 1947 using cut shoots of *Q. cerris* and *Q. robur*, and in 1948 with living material. The results obtained in both years were very similar. In 1948 experiments indicated their preference for the buds of *Q. cerris*.

On 3rd September 14 were placed on a branch of *Q. robur* but showed no interest in the buds. On the 5th 13 of them were placed on a shoot of *Q. cerris*, one inserted within 1½ minutes and within 16 minutes 7 had their ovipositors inserted, and once 12 were observed inserting at the same time. On the 13th, 11 of these insects were placed on a shoot of *Q. robur* and observed many times, but only on 7 occasions was an insect seen inserting. This was the general pattern of the other three experiments.

Only three buds on *Q. robur*, into which insects were seen inserting, developed; the others fell off, no galls formed.

In 1948 and 1949 galls of *A. circulans* formed in buds of *Q. cerris* in which insertion had taken place.

It is probable that, unless the insects placed on *Q. robur* had been prevented from escaping by the cellophane bags, no insertions would have taken place.

In 1858 Frederick Smith carried out an experiment with *A. kollari* His results are open to very grave doubt and I suspect that coincidence played a large part.

In 1950 the experiment was repeated under controlled conditions and produced negative results, though the buds used were suitable and produced spring growth. The insects showed no interest in the buds.

There is no doubt that Q. *cerris* is the legitimate host of *A. kollari*, as asserted by Beijerinck.

Six facts emerge from these experiments, as follows :

1. The upper part of the bud is selected for insertion, and during the operation the insect's head usually points upwards.

2. Some insects have no urge to insert their ovipositors into buds of *Q. cerris* when first placed on a shoot, but usually insert later.

3. Insects frequently insert within a very short time of being placed on a shoot. The longest insertion seen was 78 minutes.

4. Some insects do, at times, insert their ovipositors into buds of *Q. robur*, but this is the exception, not the rule, and it is open to doubt if insertion takes place under natural conditions.

5. *A. kollari* inserts its ovipositor freely into buds of *Q. cerris*, and in buds into which insertion had been observed, galls of *A. circulans* formed.

6. The galls produced by *A. kollari* are oblong in shape.

In 1876 E. A. Ormerod found galls of *A. circulans* on trees of *Q. cerris* in Kew Gardens. This is the first record.

During the springs of 1948–1949 experiments were carried out with *A. circulans* under the strictest control conditions. The 1948 experiments gave negative results, the bud scales on the shoots used being, perhaps, too closely imbricated to allow easy insertion of the ovipositor ; a few abortive attempts only were made.

A. circulans was observed on a bud on the oak in my garden with its ovipositor inserted, and later a gall formed in a lateral bud on the spring growth produced by the bud. The tentative conclusion was that the insect was responsible for the gall.

In 1949 a series of 10 experiments were carried out between 28th April and 17th May using branches or shoots on a tree of *Q. robur*. Galls formed in the buds of spring growth. In all 7 galls were obtained. No galls appeared in buds on spring growth from buds into which an insect had not been observed inserting. There were several failures ; in some cases it is possible to account for them.

From my observations galls always appear on spring growth. The failures with insects placed on shoots which produced spring growth might be accounted for by suggesting that the insects had not mated.

The experiment with the virgin female that not only inserted but oviposited, indicates that insertion and oviposition do not necessarily mean that copulation has taken place. From the positive results obtained it is now certain that *A. circulans*, seen inserting into the bud in 1948, was responsible for the gall that appeared later.

The controlled experiments prove conclusively that *A. circulans* is the sexual generation of *A. kollari* and is responsible for the formation of the marble gall, as asserted by Beijerinck.

Eight facts emerge from these experiments, as follows :

1. Copulation takes place in captivity and is very quickly carried out.

2. The lower part of a bud is selected for insertion and during the operation the insect's head points downwards.

3. Insects insert quite readily into buds of *Q. robur* provided they are suitable. The longest insertion seen was 68½ minutes into a bud on shoot 4, and the insect still had its ovipositor inserted when the observation ended.

4. Insertion does not take place into buds with tightly imbricated scales, though abortive attempts are often made.

5. Insertion must be into a bud that later produces spring growth, or gall formation will not take place, as galls appear in the buds of spring growth.

6. In captivity the average length of life of the male is 2.7 days and of the female 4.8, as opposed to 13.2 days for *A. kollari.*

7. The galls produced by *A. circulans,* when normally developed, are spherical in shape.

8. The spread of the marble gall, or indeed its appearance in this country at all, was made possible by the introduction of *Q. cerris* in 1735.

Since the connection between *A. circulans* and *A. kollari* has been established the nomenclature will require revision. Mr. R. B. Benson has kindly undertaken this task.

REVISION OF NOMENCLATURE.

By R. B. Benson.

Now that it is certain that *Adleria kollari* (Hartig, 1843) is the ♉ (= agamic form) of *Andricus circulans* Mayr, 1870, it is proposed that for the time being the species should be spoken of as *Andricus kollari* (Hartig) ♉, for the agamic form, and ♂ and ♀ for the sexual forms.

It should be noted that *Cynips kollari* Hartig is the type species of *Adleria* Rohwer and Fagan, 1917, and the genus *Adleria* therefore becomes a synonym of *Andricus* Hartig, 1840. The association of the alternate generations with different host-species is not known elsewhere in the Cynipidae, though Beijerinck, in addition to his studies of *Adleria kollari*, mentioned also that *Adleria quercus-calicis* Burgsdorf (on *Quercus aegilops* L., *robur* L. (= *pedunculata* Ehrh.) *pubescens* Willd. and *petraea* (Matt.) Liebl. (= *sessiliflora* Salisb.)) is the ♉ generation of *Andricus cerri* Beijerinck (on *Quercus cerris* L.) and that *Adleria infectoria* Hartig (= *tinctoria* var. *nostra*) (on *Quercus lusitanica* Lam., *robur*, *pubescens* and *petraea*) is the ♉ generation of *Andricus burgundus* Giraud (on *Quercus cerris* and *suber* L.) ; and this suggests that the ♂ and ♀ generations of still other species heretofore included in *Adleria* might likewise be found among species of *Andricus* only known as ♂ and ♀ attached to *Quercus cerris*, *suber*, etc.

If alternating host species is a feature of the whole group of species formerly included in *Adleria* then their generic status might be reconsidered ; but the only distinguishing morphological character now known is the presence of long silky pubescent clothing on the abdomen of the agamic forms, a diagnosis not applicable to the males and females.

Acknowledgments.

I wish to share the credit of resolving this long-standing problem with Mr. M. Niblett who, in 1949, also obtained galls under controlled conditions. We thus confirm each others results.

I desire to thank Mr. R. B. Benson and Mr. J. F. Perkins of the British Museum (Natural History), for naming the parasites and inquilines. I am also indebted to the following for help in various aspects of the investigation : Dr. C. R. Metcalfe of the Jodrell Laboratory, Royal Botanic Gardens, Kew, for dissecting many buds and counting and observing position of the eggs; Mr. G. Atkinson, artist to the Royal Botanic Gardens, Kew, for the figures; Dr. A. Wegener of Dauntsey's School, West Lavington, for help in plotting the occurrence of *Q. cerris* in the district, for collecting gall material, and for translating Beijerinck's paper; Mr. E. R. H. Andrews, Market Lavington, for diagrammatic drawings of the branch and shoots; two boys at Dauntsey's School, C. Reinganum for the figures of the growth of the gall, and P. H. Frankel for the photographs of the insects inserting their ovipositors; Mr. P. A. Smith, Urchfont, for constructing the talc cylinders.

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PLATE I.

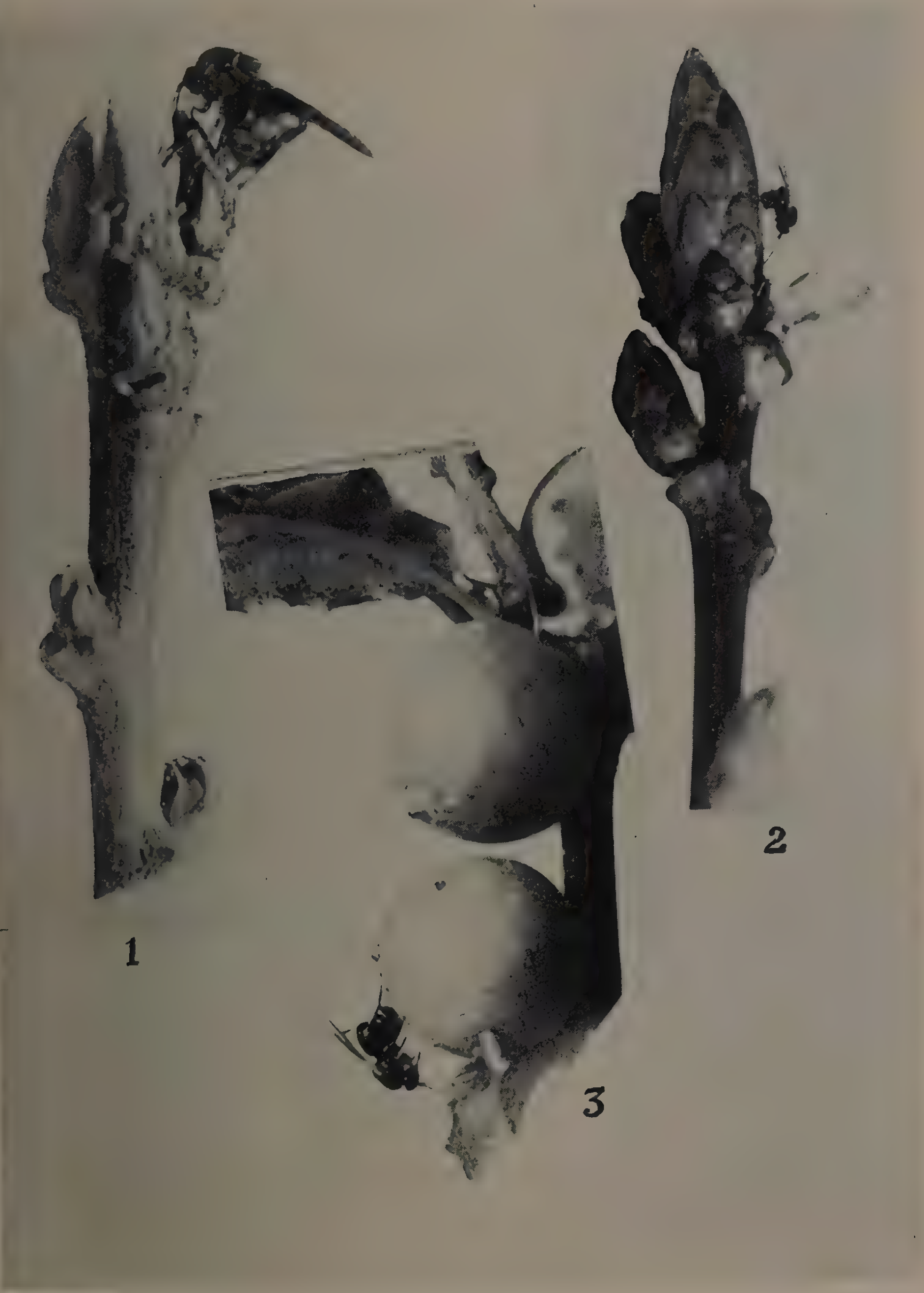
FIG. 1.—*Adleria kollari* inserting into bud of *Quercus cerris*. × 4½.

FIG. 2.—*Andricus circulans* inserting into bud of *Quercus robur*. × 4½.

FIG. 3.—*Synergus reinhardi* inserting into a Marble Gall. × 4½.

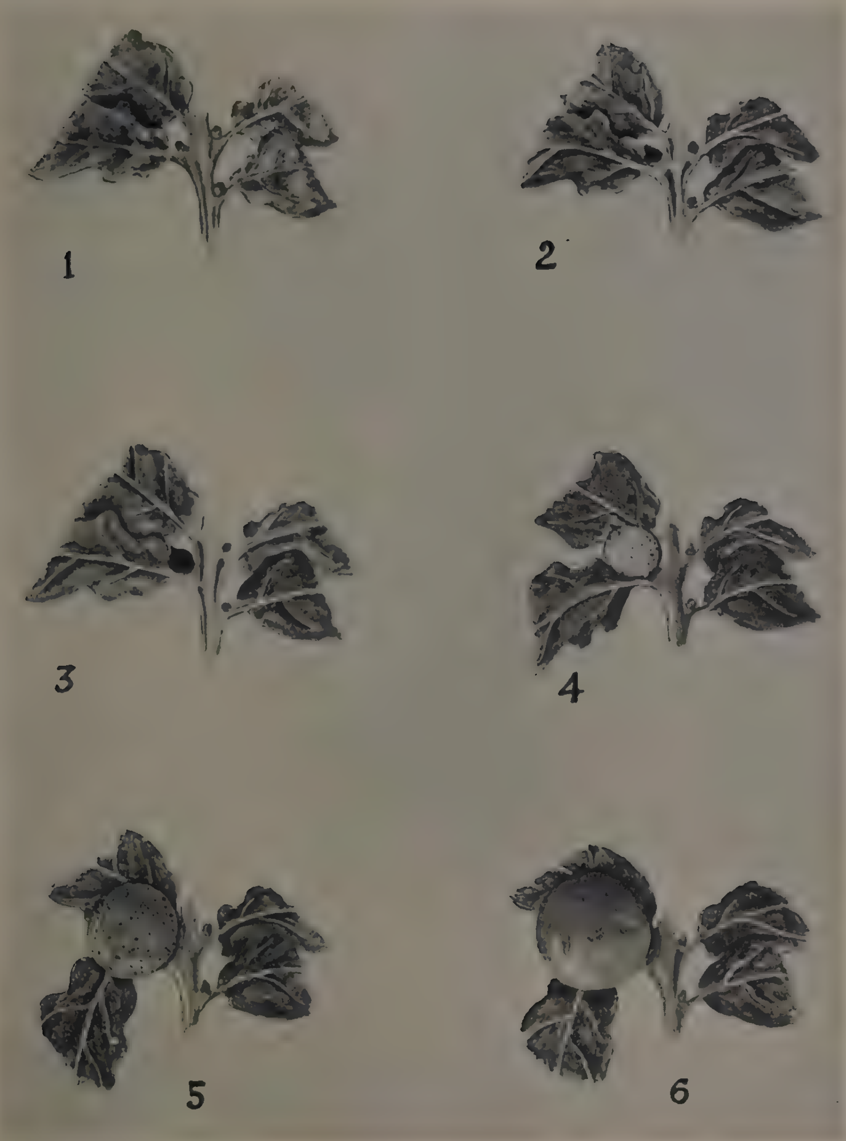
PLATE II.

FIGS. 1–6.—The development of a Marble Gall produced under control from its first appearance to maturity. (1) Gall as it appeared in left lateral bud May 28th; (2) June 7th; (3) June 12th; (4) June 20th; (5) June 27th; (6) August 22nd. Natural size.



The life-cycle of *Adleria kollari* Hartig.

E. M. Marsden-Jones. *Adlard & Son, Ltd., Dorking.*



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THE INTRINSIC RANGE AND SPEED OF FLIGHT OF INSECTS

By B. HOCKING, F.R.E.S.
(Department of Entomology, University of Alberta)

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PART. I.—INTRODUCTION AND REVIEW.

1. INTRODUCTION.

DURING the last 40 years hundreds of investigations into insect flight range have been made by the method of releasing marked specimens. The value of this method decreases in proportion to the square of the range of the species studied. Where there are no roads or trails and terrain is difficult, it is almost valueless for species which fly more than about five miles. This is the situation in northern Canada, where biting flies are known to travel distances of the order of a hundred miles, while man is often restricted to less than ten. This, too, is the situation which prompted the intrinsic approach to the problem of insect flight range followed in this study.

The energy resources of some of these northern species have been investigated (Part II), and balanced against their power requirements in flight (Part III) after considering the efficiency of utilization (Part IV), to arrive at reasoned estimates of the distance which they might travel in still air (Part V). Additional observations on the weight of the flight muscles permit estimates also of the maximum air speeds of which these insects are capable (Part VI). Similar observations have been made on the honey bee and on *Drosophila*. There is more background of physiological knowledge for these species; the data on them lend support to the specific conclusions reached, and provide a better basis for generalization from these.

Most of the field work was done in northern Manitoba, near where the great Churchill River flows into Hudson Bay at the northern limit of trees. Entomological descriptions and a map of the area have recently been published (Twinn *et al.*, 1948; Hocking *et al.*, 1950; Miller, 1951; Hocking and Pickering, 1953). The same papers include information on the bionomics of the ten species studied there. These were:

TABANIDAE:

- *Tabanus* (*Hybomitra*) *affinis* Kirby.
- *Tabanus* (*Hybomitra*) *septentrionalis* Loew.
- *Chrysops furcata* Walker.
- *Chrysops nigripes* Zetterstedt.

CULICIDAE:

- *Aëdes campestris* Dyar and Knab.
- *Aëdes communis* De Geer.
- *Aëdes nearcticus* Dyar.
- *Aëdes punctor* Kirby.

SIMULIIDAE:

- *Simulium venustum* Say.
- *Simulium vittatum* Zetterstedt.

Incomplete data were obtained on some other species. All the investigations were made on females caught in the field as adults, except where reared specimens are indicated in the text. There was no deliberate selection of specimens, but, by their nature, a preponderance of blood-hungry individuals was inevitable. None were blood fed, none were gravid, but probably all were fertilized.

The honey bees used were all Italian workers. They were of various ages, mostly from a field hive, a few from an over-wintering indoor observation hive. Only females of *Drosophila melanogaster* Meigen were used. These were reared in standard maize meal medium in half-pint milk bottles, at 70° F. Many were gravid.

C.G.S. units are used throughout except where conversion to them would mean inaccuracy or clumsiness. Conversion factors to customary units, the values of constants and standards adopted and the meanings of symbols are given in Appendix D. Where the calculation of standard errors of means was possible these are given in the tables, followed by the number of observations in parentheses : $26{\cdot}0 \pm 5{\cdot}1(20)$. Other figures in brackets in the tables are the maxima relating to the figures which immediately precede them. Figures in italics are values calculated by comparison with related species.

General aspects of animal and insect flight are reviewed at the outset. Each part opens with a brief review of work relevant to its content, and closes with generalizations applicable to other insects. A general discussion and a summary of conclusions are given at the end.

2. The Flight of Animals.

True animal flight, the controlled progression of an animal through the air, has been separately evolved on five occasions. The first of these evolutions took place in the Upper Carboniferous period, and was a dominating influence in the development of the class Insecta to its present position as the most important class in the animal kingdom. It followed so promptly, geologically speaking, on the development of abundant vertically growing plants that it is reasonable to suppose the initial steps to have been simply delayed descents, or glides from the elevations so provided. If this is true, it foreshadowed the close association between plants and insects which has been characteristic of so much of the subsequent development of each group, and which is reflected in the usual association of insect fossils with vegetable deposits. All wing movements are simultaneous. This suggests that the first fliers had a closer affinity with aquatic than with terrestrial life. Simultaneous movements are the rule in water, alternate movements on land (Grant, 1948). The last of these evolutions took place at the beginning of the 20th century, when man learnt to fly. Heavier than any flier before him, he required an auxiliary source of power.

There have been many partial adaptations to the air, from the passive transport of gossamer spiders, spores, and seeds, to the almost-flight hydroplaning of the flying fish. Lull (1906) has enumerated twelve of these. It is strange that, discounting reports of flying Crustacea (Worcester, 1914), all that come anywhere near true flight are among the vertebrates. Larger animals require more power per unit weight to maintain themselves in the air (De Lucy, 1865 ; Müllenhoff, 1885 ; Bryan, 1896), but they are endowed with less

(Hill, 1950). Thus the greater size of vertebrates places them at a disadvantage in their attempts at flight. Mallock (1909) in fact calculated, taking the power developed as proportional to the weight and equal to 10^{-3} horse-power per lb., that the heaviest animal which could maintain itself stationary in the air would weigh about $10\frac{1}{2}$ lb. If his calculation is modified in accordance with the now accepted relationship, power $\propto$ weight$^{0.73}$, this upper weight limit becomes closer to that actually found.

All successful animal fliers have used essentially similar means, both lift and propulsion being provided by one or two pairs of planes oscillating about axes inclined to and not far removed from the median longitudinal axis of the body. Even the inclined figure-of-eight movement of the wing tip, at one time considered peculiar to insects, has been demonstrated in birds (Stolpe, 1938).

Man, envying the abilities of birds, has been interested in animal flight from very early times. Unless the construction of a flying wooden model of a dove by Archytas of Tarentum (*c.* 428–347 B.C.) reported by Aulus Gellius in Book X of his *Noctium Atticarum* is accepted, the earliest significant thinking on this subject was that of Aristotle. His comments in *De incessu animalium* and *De partibus animalium* are well known. Leonardo da Vinci made many contributions in the practical field and established some aerodynamic principles (Hart, 1925). He was more interested in the flight of birds than that of insects.

Remarkable contributions were made by Borelli (1680), who, unaware of da Vinci's work, discussed fully and thoroughly the whole question of animal movement in his *De motu animalium.* This outstanding book goes into such questions as the position of the centre of gravity, the sizes and mode of operation of the muscles, and the forces acting on the wings of a flying bird. Borelli concluded from theoretical considerations that flight would be impossible for man. Auxiliary power was then out of the question. Against these positive contributions must be set his statement, later known as Borelli's Law (Miall and Denny, 1886 : 43), that the work which can be done by the contraction of a muscle is proportional to its volume. Still frequently accepted, this has contributed to the confusion in problems of locomotion at either end of the animal size scale, the swimming of whales (Gawn, 1948 ; Parry, 1949), and the flying of insects (Magnan, 1934).

Borelli so convinced the world that the 18th century brought little progress. It was not until the invention of steam and internal combustion engines in the 19th century opened the way to human flight that an intense scientific interest in the flight of animals developed. This was followed by general public attention (Ridewood, 1913) once man had begun to fly. Scientists were at first content to observe and interpret. Among the last of the early observers was Pettigrew (1868, 1870, 1871, 1873). The experimental school of Marey (1874) started at this time, and it is not surprising that his followers found much to criticize in Pettigrew's writings. They might have done better than hold up to ridicule his belief that man would one day fly (Garrod, 1874). Observers have continued to make important contributions (e.g., Peal, 1897 ; Hankin, 1914, 1922).

Photographic techniques were now being improved and were soon employed in the study of animal locomotion. The paces of the horse were first studied, followed rapidly by the flight of birds (Muybridge, 1899), and before long by that of insects (von Lendenfeld, 1903). It is not generally realized that the cinema of to-day had its beginnings in the study of animal movements. Further improvements in photographic techniques (Bull, 1904; Oehmichen, 1920; Germeshausen and Edgerton, 1937) culminated in the very satisfactory series of pictures obtained by Magnan (1934) and Chadwick and Edgerton (1939) of flying insects, and the excellent results of Brown (1948) with birds. Biological applications of high speed photography have been reviewed by Chesterman (1951), earlier French work by Thevenard and Tassel (1948), and a special issue of the *Photographic Journal* (1952, **92**B (5), Sept.-Oct.) has covered some of the latest developments.

Quite detailed and accurate information on the form and speed of wing movements is available. It is so complete indeed that flying models based on it have been constructed by von Holst and Kucheman (1942). These have remarkable stability and performance. Amid much scepticism, these authors maintain that the ornithopter or powered wing aircraft has great possibilities either in its own right, or as a means to the improvement of conventional machines. A moderately successful captive machine of this type was actually constructed by Marey as early as 1874.

Wind tunnels have only recently been used in the study of animal flight, and for quite limited purposes. Shoulejkin (1929), according to Carter (1945), used this method to determine the speed at which flying fish could obtain adequate lift. Magnan (1934), Kennedy (1939), Hollick (1940), Digby (Williams, 1949*b*) and Krogh and Weis-Fogh (1951) have used wind tunnels for various purposes with insects.

The power required by a flying animal was discussed by Fitzgerald (1899, 1910). He mentioned views as divergent as those of Navier, that the power varies as the cube of the velocity; and of Langley that it varies inversely as the velocity; obviously there is confusion here between the power required for progression and that for support. In his calculations on hovering birds, Lilienthal (1911) expressed the work done as twice the product of the weight and the mean distance travelled by the centre of the pressure of the wing. Obviously sailing flight, of which the largest fliers must be capable if they are to fly at all, must be considered separately from flapping flight, since in the former the kinetic energy of the natural movement of the air is utilized. This is so variable that the power required for sailing flight scarcely admits of mathematical treatment. Measurements of metabolic rate in flight have given a better idea of the power requirements of insects and birds (Pearson, 1950) than estimates on a physical basis. The metabolic rate of bats has been measured only in relation to hibernation and thermoregulation (Hock, 1951). Theories of animal flight have hardly kept pace with practical studies, the difficulties being more on the physical than the biological side; thus Magnan (1934) was unable to fit a theory to his extensive experimental data. The statement of Rashevsky (1944) that "even a remotely exact theory of flight of birds and insects meets with almost insuperable difficulties at present" seems, however, a little conservative. Bibliographies of animal flight giving over 2000 titles have recently been issued (Anon., no date; FitzPatrick, 1952*b*).

3. SPECIAL FEATURES OF INSECT FLIGHT.

(a) *Morphology.*—General studies of the morphology of the insect pterothorax have been made by Graber (1872), Snodgrass (1909, 1927, 1929) and by

Ritter (1911). Certain special aspects of morphology in relation to flight have been studied by Komarek (1929). He considered the reduction in number of the abdominal segments in the Diptera to be significant in permitting greater skill and power in flight, through a forward movement of the centre of gravity. Lanham (1951) has discussed the influence of venation on the aerodynamic qualities of wings in the higher Hymenoptera. He associated lobes on the trailing edge of wings with rapid and precisely controlled flight in this group and in the Diptera. General morphological studies of *Tabanus sp.* have been made by Bonhag (1949, 1951), of the honey bee by Snodgrass (1910, 1925), and of *Drosophila* by Zalokar (1947). A histological account of the musculature of the bee has been given by Morison (1927).

(b) *Wing movements.*—Early observers concentrated on the movements and flexions of the insect wing and thorax during flight. Chabrier (1820) considered that the venation enabled the wings to get a grip on the air, and that the air sacs permitted the rapid removal of the heat generated. Agassiz (1858) supposed that in the Lepidoptera the wings became separated during the upstroke, permitting the passage of air between them, as between the primary feathers of a bird's wing.

Nearly ten years earlier than Marey's experimental work with birds Plateau (1865, 1866) studied the weights which could be lifted by the flying insect. More important than this direct contribution, this versatile investigator laid the foundations of insect physiology, and thus prepared the way for more profitable studies of flight. It is surprising that he did not apply his father's invention, the stroboscope, to the study of wing movement. This had to wait 25 years (Marey, 1890), and the method was not extensively used for 55 years (Oehmichen, 1920).

Janet (1899) concluded that there is no flexion of the scutum or scutellum during flight, but a bending of the one on the other. Marey (1874) and Bull (1904) considered the figure-of-eight movement of the wing to be brought about by air pressure. Lendenfeld (1885) and Oehmichen held that the subsidiary wing muscles were responsible for this. Chadwick (1940) has shown that the Odonata have obtained efficient flight, without concentrating on a single pair of wings, by the simple expedient of having the hind wings always moving ahead of the fore wings, so that they do not encounter the disturbances caused by these. Boettiger and Furshpan (1952*b*) have described two new methods of investigating flight movements.

(c) *Wing loading.*—Early writers considered the wing area per unit of weight to be a measure of the flying ability of an insect. Data on the wing loading of insects have been compiled by Demoll (1918), Portier and Rorthays (1926), and Piéron (1927). On this basis it soon became clear that the smaller insects would always rate as the better fliers, since the wing loading increases regularly with the span (Hankin, 1922). Müllenhoff (1855) introduced the concept: wing area$^{\frac{1}{2}}$ × weight$^{\frac{1}{3}}$ as a measure of flying ability. Prochnow (1928) pointed out that this really expresses the gliding ability, and that the wing-beat frequency must be included to express flying ability.

(d) *Wing-beat frequency.*—The outstanding peculiarity of insect flight is the very high frequency of wing beat in many groups. This is associated with the buzzing of insects (Lutz, 1902; Weber, 1906; Aubin, 1914), and has provoked many investigations (Burmeister, 1841; Voss, 1914; Buddenbrock, 1916;

Reed *et al.*, 1942; Williams and Chadwick, 1943; Boettiger and Furshpan, 1950). There are also sections on wing-beat frequency in general works on flight referred to elsewhere. The subject has been critically reviewed by Sotavalta (1947), who has made good use of his remarkable sense of absolute pitch to contribute a vast amount of additional information (1947, 1951). Many of the early figures for frequency were conflicting on account of two major errors, the soprano-tenor error and the mistaking of harmonic overtones for the true frequency. The effect on frequency of various external and internal factors, especially temperature, has been studied by Roch (1922), Chadwick (1939*b*), Williams (1941), Aboul-Nasr (1950) and Sotavalta (1952). As Gaul (1951) pointed out, the temperature of the wing muscles during flight may be much higher than the ambient temperature.

Several attempts have been made to derive an expression for the frequency of wing beat in terms of the weight and wing dimensions of the insect, either from theoretical considerations (Attila, 1947) or from practical data (Magnan and Sainte-Laguë, 1932, 1933; Sotavalta, 1947, 1950, 1952). These expressions can be written in the general form:

$$F = k.\ W^x S^y L^z,$$

where W is the weight of the insect, L the wing length or the moment of inertia of the wing, and S either the wing area or the angular amplitude of wing beat. Opinions differ regarding the values of x, y and z. These expressions give, at best, only an approximate figure for the frequency.

The conflict between the frequency of insect wing beat and the maximum frequency of contraction of isolated muscle has long been a problem. This has been partially solved by the work of Pringle (1949), Roeder *et al.* (1949), Roeder and Weiant (1950), Roeder (1951) and Boettiger (1951). These investigations have shown that for high wing-beat frequencies action potentials representing nerve stimuli to the flight muscles occur at a much lower frequency than the contractions of the muscles. It seems clear that both the wing muscle system and the haltere and muscle system in the Diptera vibrate at their own resonant mechanical frequency. Were this not so, the energy loss from the repeated changes in the direction of wing movement would surely be impossibly high—much higher than Chadwick (1951) found. The Weber brothers claimed as long ago as 1836 (Thompson, 1942) that the natural or pendulum frequency of an animal appendage governed the frequency of its movement. This has apparently not been applied specifically to insect wings. This frequency depends only on the moment of inertia of the system, and the dimensions and elastic moduli of the terga and flight muscles, but may be modified by air damping. Variations in frequency could be brought about by nerve stimuli or enzyme changes (Levenbook and Williams, 1951) affecting the elastic constants of the flight muscles, and by the action of the subsidiary wing muscles causing variations in the stroke pattern and hence in the air damping. Pringle, however, only advanced a resonant hypothesis specifically for the halteres, and found it necessary to postulate an antagonistic action between the two sets of flight muscles, which each contract *actively* (my italics, B. H.) in response to being stretched by the other pair. An alternative explanation is possible; the stroke immediately following the action potential is powered biologically, while the contractions on intermediate strokes are only active in the sense that a stretched spring contracts actively. The demonstration of a slightly decreasing amplitude between successive nerve stimuli would prove this.

If this theory is correct, a more accurate synthetic expression for the frequency should be possible by substituting the dimensions of muscles and pterothoracic terga for the weight of the insect. Data on the elastic moduli of other muscles have recently been obtained by Buchthal (1942) and Johnson and Perkins (1951), and Pierce (1948) has speculated regarding the values for the terga and wings.

The histology and the biochemistry of the flight muscles of higher insects exhibit certain peculiarities (Watanabe and Williams, 1951; Ishimoto and Williams, 1949), which have led to the name *fibrillar* being used for them (Williams and Williams, 1943). These may be connected with elastic peculiarities, or with peculiarities of elastic change in response to nerve stimuli.

In the beginning, the rush of air past the paranotal lobes of the gliding ancestor may be supposed to have started vibrations in these in the same way as blowing a wind instrument causes the reed to vibrate. Such vibrations must surely have been at the mechanical frequency.

(e) *The forces acting on the flying insect.*—Shortly after Plateau's work on lifting ability, Krarup-Hansen (1869) discussed the flight of butterflies and dragonflies and made a brief calculation on the forces involved. The next important contribution was that of Axenfeld (1911). He made a remarkable study of the work which insects could do in flight by harnessing them to an arm operating a small winch. His data are used in Part IV. Sporn (1925) studied the length and height of the leaps of grasshoppers, and the power required for these. Hollick (1940), working with *Muscina stabulans*, demonstrated that there were no essential differences between the wing movements in free flight, and those of the same insect held stationary in a stream of air. He measured the direction and magnitude of the force resulting from wing action. This usually cut the longitudinal axis behind the centre of gravity, and had a vertical component insufficient to support the insect. Von Holst (1943, 1948) studied the forces acting on small oscillating plates, and calculated values of Reynolds' number for flying insects. These are small, usually less than 5000, indicating laminar flow, and that the viscosity forces are relatively more important than they are to birds and aircraft.

(f) *Stability and control.*—The problems of stability and steering in insects have only recently received much attention. Osborn (1912) considered that backward flight was obtained by a rotation of the wing about a vertical axis through its base. Bervoets (1912, 1914) studied the significance of the pterostigma, which he regarded as an unknown sense organ, but not a stabilizer. Stellwaag (1916) concluded that steering, both vertically and horizontally, was by means of unilateral changes in the plane of vibration, with or without changes in amplitude, rather than by a movement of the centre of gravity. Boettiger and Furshpan (1952*a*) found that the indirect muscles played little part in steering or amplitude changes. The stabilizing functions of the campaniform sensilla and the halteres have been discussed by Melin (1941); Pringle (1948) showed that they serve as yaw indicators. Sensory hair patches on the heads of grasshoppers serving as flight regulators were described by Boyd and Ewer (1949) and by Weis-Fogh (1949, 1950*b*). Waterman (1950) has reviewed work on sense organs used in flight, and drawn an analogy with aircraft instrumentation.

(g) *Insect migration and flight range.*—The range of flight of which insects are capable is of interest in zoogeographical studies ; the distances which a species habitually flies are of significance in evolution. The migrations of animals have attracted so much attention in recent years that their study constitutes a subject in itself, although closely related to zoogeography and to evolution. Finally, the range of flight of insects which transmit diseases is of great practical importance. In general there can be no transmission of a disease unless the flight range of the vector or carrier is greater than the reciprocal of the square root of the population per unit area of the host, that is unless $PR^2 > 1$, where P is the host population per unit area and R the flight range of the vector. This rule breaks down only for pathogens which are transmitted through the egg of the vector.

Until this last practical significance of flight range was appreciated, that is, until Ross had demonstrated the essentials of the *Plasmodium* life-cycle, no serious attempts at determining insect flight range were made. Ross himself soon saw the importance of flight range, and his remarks on the subject (Howard, Dyar and Knab, 1912, p. 212) show a better appreciation of the problems involved than do many more recent discussions. He apparently occasioned the remarkable mathematical study by Pearson and Blakeman (1906), in which the experimental determination of flight range by the method of marking, release and recapture was suggested. The same authors distinguish between a *flight* from origin to oviposition site, and a *flitter* " a mere to-and-fro motion associated with the quest for food or mate in the neighbourhood of the habitat." This distinction is a biological reality in many groups of insects (e.g., Zulueta, 1950).

As Kettle (1951*a*) has pointed out, the term " flight range " has been much misused, often taking the place of the regression of population density on distance from a centre of dispersion (Wadley and Wolfenbarger, 1944). This is dependent on flight range, flight habits, and emergence spectrum, and gives a more complete picture of the dispersion of an insect population. The term will be used here to indicate the maximum distance which the average members of an insect species may traverse in still air, without feeding. The application of a knowledge of flight range in this sense requires information on the vector sums of wind velocities at various places on and above the earth's surface. A knowledge of the flight habits of the species concerned, in particular the influence of wind in determining flight direction, is also needed. This information and knowledge is becoming increasingly available (Wellington, 1945 ; Kennedy, 1951 ; Rainey, 1951 ; Waloff, 1953), much of it as a result of studies of migration (Williams, 1923, 1930 ; Abbott, 1950, 1951).

The term " migration " is used in its now generally accepted sense, an extensive directional movement, with or without return to the origin. The proposal by Heape (1931) to restrict the term to a there-and-back movement, using *emigration* for movements without return, has proved untenable. Students of insect migration disagree regarding the importance of determinate flight in these movements. Williams (1949*a*), studying mainly butterflies, reservedly considers the direction of movement to be largely determined by the insect. Most observers of the larger species incline to this view (Shannon, 1916 ; Lack and Lack, 1951). Felt (1925*a, b*, 1926, 1928), on the other hand, considered migrations to be simply random movements, directionalized by wind and other conditions. He attributed dispersal to currents in the upper air. Much of the evidence on the smaller insects supports this view, but by no means all of it. In particular, support has been taken from many of the recent studies of aerial plankton, in which small insects are associated with many organisms without wings (Hardy and Milne, 1937, 1938*a*, *b* ; Cockerell, 1939 ; Glick, 1939, 1942 ; Wolfenbarger, 1946 ; Gislén, 1948 ; Johnson, 1951).

PART II.—THE ENERGY AVAILABLE TO THE INSECT.

Many reviews of insect nutrition contain information which can be used in a consideration of the energy resources of adult insects (Uvarov, 1929 ; Babers, 1941 ; Trager, 1947 ; Brues, 1946 ; Wigglesworth, 1950). A knowledge of the exact chemical nature of the energy reserves is not required inasmuch as the energy values of the different representatives of the main groups of food materials are essentially similar. Furthermore, since there is no evidence that any insect is able to utilize proteins to provide the energy required for flight, a knowledge of the fat and carbohydrate resources is sufficient. Of these two groups carbohydrates are much the more important in the insects studied here. Although the utilization of fats for flight has been demonstrated in locusts (Krogh and Weis-Fogh, 1951), and indicated in leaf-hoppers (Fulton and Romney, 1940 ; Cook, 1944) and some Lepidoptera (Williams, 1945 ; Beall, 1948), the evidence both from measurements of the respiratory quotient (Chadwick, 1947) and from the changes in food reserves (Williams *et al.*, 1943 ; Wigglesworth, 1949) all points to the utilization of carbohydrates alone in the Diptera.

The problem of evaluating the energy resources of the adult blood-sucking flies falls into three parts ; firstly a consideration of the resources within the tissues, the balance of supply over expenditure from the immature stages plus additions to this from adult feeding ; secondly the measurement of the capacity of the insect for supplementing this by food stored in the crop ; and thirdly the investigation of the energy value and availability of food in the normal habitat of the adult insects.

1. Chemical Reserves within the Tissues.

(a) *Review.*—On emergence these reserves represent the balance of larval feeding over requirements in the larval and pupal stages. There is tremendous variation in their extent between species. Insects which do not feed as adults, such as *Gasterophilus* and many Lepidoptera, must carry into adult life a sufficient balance for the whole of their quite considerable activities (Levenbook, 1951). On the other hand, insects with active pupae like mosquitoes and some Trichoptera may reach the adult stage with very slender resources.

A detailed study of the protein, fat and glycogen metabolism in the larvae of *Aëdes aegypti* has been made by Wigglesworth (1942). He found all these materials to be stored in quantity; but under laboratory conditions, in the absence of further feeding, these reserves were used up within 10–14 days after moulting to the 4th instar. Smorodinzew and Bebechine (1939) investigated the fat content of adult *Taeniorhynchus saginatus*, and found 0·275 per cent. cholesterol and 1·07 per cent. phosphatides calculated as lecithin. De

Boissezon (1929) found a carry-over of protein from the larva in *Culex pipiens*; this contributed to the development of the eggs. Bettini (1947), however, found no protein storage in the fat body of *Anopheles m. atroparvus*, even after a blood meal.

Filter feeding, especially in water containing little suspended organic matter, would not appear to favour the accumulation of large reserves, but the energy requirements also seem to be small (e.g., Jørgensen, 1952). No quantitative study has been made on insects, but Büttiker (1948) investigated the depths of larval diving, and Thomas (1950) studied the stimuli which evoke diving in *Culex fatigans*. He found these to be water vibrations or changes in light intensity, and attributed the diminished response of older larvae to increasing oxygen requirements; this could equally well be due to an increased need for conserving energy. Similar observations have been made on the species of *Aëdes* studied here (Hocking, 1953*b*), but it might be added that the vigorous wriggling activity regarded as so typical of mosquito larvae appears to be mainly an escape reaction, rarely indulged under natural conditions. The mouth-brush vibration which creates the feeding current serves also for most locomotory requirements and is much more economical of energy.

In the Simuliidae, Pacaud (1944, 1950) found glycogen storage in the mesenteron of the larvae of *Simulium costatum* Fried. similar to that found by Wigglesworth in *Aëdes*, but there are no data on the extent of chemical reserves at the time of pupation. Hora (1927) and Grenier (1945) discussed the mechanism of locomotion of *Simulium* larvae and reviewed earlier work on this, but there is no indication of its extent. Hocking and Pickering (1953) draw attention to the very low energy requirements of northern species of *Simulium* during larval life and suggest that the energy legacy is also small. The many reports of phoretic association of African species with mayfly nymphs (Ribeiro, 1854; Grenier, 1950) and with crabs (van Someren and McMahon, 1950; McMahon, 1951, 1952) which is apparently obligate, suggest that these tropical black-fly larvae too have an energy problem.

Less is known of the energy relationships of the Tabanidae. The larvae of some of the species studied live at the margins of shallow swampy pools, where they prey on aquatic organisms which become stranded as the water recedes, and on terrestrial organisms which get into difficulties as the water advances. This advantageous habitat and their larger size suggest that they have less of a problem than the black flies. Hatton (1948), however, described remarkable activity by mature tabanid larvae which have finished feeding.

The immature stages of the honey bee indulge in no locomotory activity and little activity of any kind, so that energy is required only for resting metabolism. Worker larvae are adequately fed, although the quality of their food is restricted. Bertholf (1927) studied the utilization of carbohydrates by bee larvae. Parhon (1909) found from 0·14 to 0·21 per cent. of glycogen on the live weight of the adult. Beutler (1937) found 0·3 to 0·9 per cent. Presumably the economy of the hive renders anything more than short-term storage within the body of the insect unnecessary.

There is much information on the nutritional needs of *Drosophila* larvae, and on the reserves present in the newly emerged adults (Wigglesworth, 1949), although there is little on the activity of larvae. Williams *et al.* (1943) found recently emerged flies of *D. funebris* capable of 26 minutes flight, and correlated this with the presence of 2·5 per cent. of stored glycogen.

Reserves in *Drosophila* are increased considerably during the first few days of adult life ; glycogen reaches 4·88 per cent. of the live weight at 4–5 days in *D. funebris* (Williams *et al.*, 1943), and the duration of stationary flight reaches 4–5 hours at 1 week in *D. melanogaster* (Wigglesworth, 1949). In the other groups studied there seems to be little increase ; in the bee, presumably because of storage at the colony level, in the biting flies perhaps because short-term storage is more in keeping with the short northern summer.

(b) *Experimental.*—The experimental work on this question falls into three parts : histological examination for fat and glycogen, comparison of the average weight of specimens with the crops emptied with that of specimens flown to exhaustion, and the direct determination of the distances newly emerged specimens may fly.

Specimens newly emerged in the field, not more than 6 hours' adult age, were fixed in Carnoy's after making a median dorsal incision. Black flies and *Aëdes communis* were divided sagittally into two halves, one of which was stained in Best's carmine and the other in light green and iodine. For the other mosquito species it was necessary to remove organs and tissues and mount them separately ; the tabanids were embedded and sectioned. The same staining techniques were used. In no species was anything more than a rather sparse sprinkling of glycogen found, principally in the fat body, the flight muscles and the halteres. Compared with *Drosophila* the fat body is poorly developed in all the other species. Most glycogen was found in the mosquitoes and least in the black flies. There was little variation between specimens, or between species within each family ; none had anything approaching the proportion of glycogen found by Wigglesworth (1949), who used this technique on *Drosophila*. A similar study was made of the fat reserves in one species from each group ; the material was fixed in Bouin's and stained in Sudan Black B. Fat reserves were also small in all groups, especially the mosquitoes, and were located almost entirely in the fat body and the mid gut.

A few specimens of the two *Tabanus* species, caught in the field and of unknown age, and a few which had flown to exhaustion (Part IV, Section 2) were examined in the same way. Slightly more glycogen and fat was found in the field-caught specimens. In the exhausted specimens compared with these no change could be detected in fat deposits, but very little glycogen remained.

The average weight after flying to exhaustion was, for every species studied in this way, less than the average weight of field-caught specimens after the weight of nectar found in the crop had been subtracted. The weight of the exhausted insect is referred to as the basic weight ; that of the insect with crop empty as the empty weight. The difference between these weights can only represent the combined weight of carbohydrate utilized and moisture lost in flight. Faeces were rarely passed during flight experiments (Part IV) except by the honey bee. Weis-Fogh (1952*b*) has shown that glycogen stored in insect tissues is hydrated to 3·7 times its dry weight, and since most of the tissue storage in all species studied except the bee is glycogen, it is provisionally supposed that the difference between the empty weight and the basic weight represents mainly hydrated glycogen.

The direct determination of the distances which specimens unfed as adults could fly (Part IV, section 2) proved difficult, and data were obtained only for one specimen of *T. affinis* (16/0, Appendix C), two of *T. septentrionalis* (4/0, 5/0), one of *S. venustum* (3/0), and two of *Drosophila* (7/0, 10/0, Appendix C). *Drosophila* flew faster on its tissue reserves of glycogen than on fed sugars ; all the other species flew more slowly. All the results indicate rather less glycogen than suggested by the difference between basic and empty weights. The discrepancy is least in the smallest species, and increases steadily with increasing size. This is in agreement with the supposition that the larger species, with a smaller ratio of surface to volume, require to evaporate more water to get rid of the heat generated in flight.

TABLE I.—*The energy reserves within the tissues. All weights in mg.*

Species.	Mean weight with crop empty.	Mean exhausted weight (basic weight).	Empty weight minus basic weight.	Weight of glycogen calculated from duration of flight.	Water loss per mg. glycogen consumed.	Weight of tissue reserves expressed as glucose.
Tabanus affinis .	*161·7±9·8 (23)	142±17·8 (15)	19·7	2·37	7·3	2·66
T. septentrionalis .	61·8±9·5 (21)	54·3±4·9 (5)	7·5	1·13	5·6	1·27
Chrysops furcata .	26·0±5·1 (20)	*22·9*	*3·1*	*0·48*	*5·4*	*0·54*
C. nigripes . .	21·34±3·7 (24)	*18·8*	*2·54*	*0·40*	*5·4*	*0·45*
Aëdes campestris .	6·72±1·32 (22)	*5·22*	*1·50*	*0·24*	*5·3*	*0·269*
A. communis . .	3·11±0·50 (21)	*2·42*	*0·69*	*0·11*	*5·2*	*0·124*
A. nearcticus . .	3·15±0·44 (21)	2·45±0·34 (9)	*0·70*	*0·11*	*5·2*	*0·124*
A. punctor . .	5·77±1·1 (21)	*4·49*	*1·28*	*0·20*	*5·3*	*0·225*
Simulium venustum .	2·53±0·55 (20)	2·40±0·21 (7)	0·13	0·0212	5·1	0·0238
S. vittatum . .	2·06±0·42 (20)	*1·95*	*0·11*	*0·018*	*5·1*	*0·0205*
Apis . . .	105±8·7 (20)	83·3±2·9 (7)	21·7	†*0·6*	†*5·7*	*3·18*
Drosophila . .	0·866±0·062 (11)	0·55±0·067 (8)	0·316	0·067	3·7	0·075

Italic figures are expected values derived by calculation from experimental figures for other species in the group.

* Mean of 23 readings 161·7, standard error 9·8 ; this notation is used throughout the tables.

† Calculated from data of Beutler (1937).

It is assumed that the percentage of glycogen is the same in the other members of each family as in those studied in this way, and that the amount of extra water lost by the mosquitoes is intermediate between the amounts lost by the black flies and by the tabanids. The adopted weights of tissue reserves, expressed as glucose to simplify later calculations, together with the empty and basic weights of each species are given in Table I. Beutler (1937) has shown that in the bee most of the tissue reserves are in the form of blood sugar, probably glucose, which may reach a concentration of 10 per cent., so that the 21·7 mg. mean weight loss of the bee appears to be made up of about 0·6 mg. glycogen, 2·5 mg. blood sugar, about 16 mg. water evaporated, and the balance, faeces (Table I).

(c) *The water and temperature relations in flight.*—If both the insulating value of scales and the additional heat losses by convection and conduction are neglected, the radiant energy lost from the thorax of a mosquito may be calculated from the Stefan-Boltzman law to balance the maximum energy converted by the flight muscles (Part IV) if the surface temperature of the thorax is about 1° C. above its surroundings. Even for *T. affinis* a temperature difference of about 8° C. would be sufficient. Most of the water loss in flight thus appears to be an unavoidable feature of respiratory ventilation rather than necessary to prevent an excessive rise in body temperature. If water loss is incidental, it may be supposed to be greatly reduced as the water content of the insect becomes lower. The rates of water loss indicated in the last section are thus probably abnormally high, since they were necessarily determined on newly emerged specimens, in which the water content is high.

To obtain more information on this question, six specimens of *Drosophila*, 3 days old, were mounted, weighed, and allowed to fly without forward movement for 103 minutes (until the first specimen stopped), and re-weighed. The total weight loss was 0·475 mg., the expected total glucose consumption calculated from the average rate given by Wigglesworth (1949) was 0·098 mg., equivalent to 0·323 mg. hydrated glycogen, so that an additional 0·152 mg. of free water was lost, that is, a total of 4·5 gm. of water per gramme of glycogen utilized. The temperature was 75° F. and the saturation deficiency 16·4 mm. Hg., so that here again the water loss may have been abnormally high.

The oxidation of one gramme of glycogen produces 4200 calories; about a third of this heat would be removed by the evaporation of the water of hydration associated with it. The water associated with glycogen and sugars in storage would thus probably meet the needs of evaporative cooling in most insects. Insects which fly on fats, which have no water associated with them in storage, may, however, experience water shortage on long flights. This applies particularly to flights at high temperatures and to large insects. The water needed may be obtained by means other than drinking; water vapour may be absorbed from the air (Wigglesworth, 1950), liquid water may be absorbed through the skin (Nutman, 1941), or that produced by the metabolism may be utilized (Buxton, 1930). Weight for weight, fats produce more "metabolic water" than other fuels. In the areas to which these studies particularly relate liquid water is all too abundant, and no problem is likely to arise. Long flights over salt water raise the interesting question of the possibility of utilizing this. Butterflies have often been reported resting on the surface of the sea (Williams, 1930, p. 342), they probably utilize stored fats, they are known to drink sweat which contains much salt (Norris, 1934), and they have rectal glands which might permit the selective absorption of water, although these are not particularly well developed.

2. Adult Feeding Habits and Food Capacity.

(a) *Review.*—The discovery of the pollination of flowers by insects has been generally credited to Kölreuter (1761–6): Grant (1949), however, drew attention to a prior statement on this subject by Dobbs (1750). Since that time there have been several monumental studies (Müller, 1873 ; Darwin, 1900 ; Knuth, 1906 ; Robertson, 1928) of the significance of this association to plants, but its significance to insects has been neglected. All of the insects studied here, except perhaps *Drosophila*, normally obtain the carbohydrates which they utilize for flight in the form of nectar from flowers. Flower visiting by the honey bee is sufficiently well known to need no discussion. With the biting flies, however, although it has long been recognized that both males and females of these insects feed on nectar, little is known of the extent of this feeding. This is partly because a human observer may prove more attractive than the flowers ; partly because the biting flies may make the observation of insect visitors to flowers an unpleasant task. The information available in the literature is summarized in Table II ; 18 of the 44 records for tabanids were on umbellifers ; these flowers, and the willows, also account for 8 of the 17 records for black flies. Bradley (1931) found that anopheline mosquitoes were not attracted to leguminous plants, and did not feed to any extent on either the blossoms or the foliage. Muirhead-Thomson (1951) stated that in the field the indications are that the vast majority of females feed on blood and blood alone. Many of the mosquito species which have attracted attention as flower visitors are noteworthy on account of their flight range († in Tables II and XIII).

TABLE II.—*A summary of published records of flower visiting by biting flies.*

Insect species.	Plant species.	Author.
TABANIDAE :		
Chrysops caecutiens	Gypsophila paniculata	Müller,1873
	Mentha aquatica	
	*Pimpinella Saxifraga	
	Potentilla fruticosa	
	Brassica Kaber	Knuth, 1906
	Spiraea salicifolia	
	S. sorbifolia	
	S. ulmifolia	
	Thymus Serpyllum	
C. indus	*Heracleum maximum	Robertson, 1928
C. striatus	Achillea Millefolium	,, ,,
	*Cicuta maculata	
	Eupatorium serotinium	
	*Heracleum maximum	
	Lespedeza virginica	
	Salix interior	
	*Sium suave	
	*Peucedanum sativa	
Haematopota pluvialis	Knautia arvensis	Knuth, 1906
Silvius vitula	Eupatorium cannabinum	,, ,,
Tabanus affinis	Salix sp.	Miller, 1951
T. auripilus	*Daucus Carota	Knuth, 1906
T. borealis	*Imperatoria Ostruthium	,, ,,
	*Chaerophyllum Villarsii	
T. bovinus	Tilia ulmifolia	,, ,,
T. bromius	*Peucedanum oreoselinum	,, ,,
T. illotus	*P. sativa	Robertson, 1928

TABLE II.—*A summary of published records of flower visiting by biting flies*—(continued).

Insect species.	Plant species.	Author.
T. infuscatus	**Angelica sylvestris*	Knuth, 1906
	**Peucedanum Oreoselinum*	
	**Daucus Carota*	
T. lineola	*Cassia Chamaecrista*	Robertson, 1928
T. luridus	*Valeriana officinalis*	Müller, 1873
T. micans	**Pimpinella Saxifraga*	,, ,,
	Thymus Serpyllum	
	Allium rotundum	
T. rhombicus	*Geranium caespitosum*	Clements and Long, 1923
T. rusticus	**Heracleum Spondylium*	Müller, 1873
	Achillea Millefolium	
	Cnicus arvensis	
T. septentrionalis	*Ledum sp.*	Miller, 1951
T. tropicus	*Ajuga reptans*	Knuth, 1906
Tabanus spp.	*Thymus Serpyllum*	,, ,,
	**Cicuta maculata*	Robertson, 1928
	**Eryngium yuccifolium*	
CULICIDAE:		
†*Aëdes campestris*	*Solidago sp.*	Philip, 1943
A. cantans	*Salix pentandra*	Nielsen and Greve, 1950
	Crataegus Oxyacantha	
A. capsicus (♂ and ♀)	*Chrysanthemum vulgare*	Natvig, 1948
A. caspius	*Tanacetum vulgare*	Larsen, 1948
A. communis	*Taraxacum vulgare*	Wesenberg-Lund, 1920
	Salix arctophila and	West and Jenkins, 1951
	1 or more of:	
	Ledum decumbens	
	Rhododendron lapponicum	
	Dryas integrifolia	
	Rubus Chamaemorus	
	Habenaria obtusata	
A. detritus	*Tanacetum vulgare*	Larsen, 1948
A. nigripes	*Smilacina racemosa*	Robertson, 1928
A. punctor	*Habenaria hyperborea*	Hocking *et al.*, 1950
	Tanacetum vulgare	Larsen, 1948
†*A. sollicitans*	*Prunus sp.*	Smith *in* Knab, 1907
†*A. spenceri* (♂ and ♀)	*Salix sp.*	Knab, 1907
	Solidago sp.	Philip, 1943
A. stimulans	*Smilax herbacea*	Graenicher *in* Knab, 1907
	S. hispida	
	Asclepias syriaca	Robertson, 1928
A. vexans	*Solidago juncea*	Graenicher *in* Knab, 1907
	S. canadensis	
	S. lanceolata	
(♂ and ♀)	*Spiraea alba*	Hearle, 1926
	Solidago sp.	Philip, 1943
	Symphoricarpus orbiculatus	Robertson, 1928
	Tanacetum vulgare	Larsen, 1948
Aëdes spp.	*Rhododendron lapponicum*	Hocking *et al.*, 1950
	Ledum palustre	
	Dryas integrifolia	
	Habenaria obtusata	
Aëdes sp.	*H. obtusata*	Raup, 1930

TABLE II.—*A summary of published records of flower visiting by biting flies*—(continued).

Insect species.	Plant species.	Author.
Anopheles aquasalis	*Bidens pilosa*	Senior-White, 1952
	Mimosa pudica	
	Capraria biflora	
	Hamilea patens	
	H. erecta	
(♂ and ♀)	*Eupatorium inulifolium*	
	E. odoratum	
	Cordia macrostachya	
	Borreria verticillata	
Anopheles sp. ?	*Mentha aquatica*	Willis and Burkill, 1895
Culex albopunctulatus	?	Ficalbi *in* Knab, 1907
†*C. pipiens*	*Cnicus arvensis*	Britten, 1937
	Rhamnus Frangula	Müller, 1873
	Lopezia coronata	
	Tanacetum vulgare	Larsen, 1948
C. apicalis	*Solidago sp.*	Philip, 1943
†*C. tarsalis*		
Culiseta inornata		
C. annulatus	*Vinca sp.*	Theobald *in* Knab, 1907
	Erysimum sp.	
†*Mansonia perturbans*	*Cnicus arvensis*	Britten, 1937
Megarhinus septentrionalis	*Hydrangea arborescens*	Knab, 1907
Mosquitoes, unspecified :		
	Ceanothus americanus	Robertson, 1889
	Compositae	Theobald *in* Knab, 1907
	Salix sp.	Giles, 1902
SIMULIIDAE :		
Eusimulium furculatum	*Salix cordifolia*	Hocking and Pickering, 1953
(♂ and ♀)	*Achillea Millefolium*	
	Rubus acaulis	
†*Simulium damnosum*	Orchidaceae or Asclepiadaceae	Lewis, 1953
†*S. griseicolle*	?	,, ,,
S. pecuarum	*Sassafras variifolium*	Robertson, 1928
S. venustum	**Cicuta Mackenzieana*	Hocking and Pickering, 1953
	**Heracleum maximum*	
(♂ and ♀)	*Rubus acaulis*	Müller, 1873
	Achillea Millefolium	
Simulium sp.	*Chrysosplenium alternifera*	
	Adoxa Moschatellina	
	Salix viminalis	Knuth, 1906–9
	Prunus serotina	Robertson, 1928
	Salix cordata	
	S. interior	
	**Chaerophyllum procumbens*	
	**Zizia aurea*	

* Umbelliferae.
† Reputed migrant species ; see Table XIII.

All records female except where indicated.

Nielsen and Greve (1950) found *Aëdes cantans* taking morning and evening meals of nectar; Larsen (1948) attributed this periodicity in other species to diurnal weather changes. Twinn *et al.* (1948) and Hocking *et al.* (1950) estimated the percentage of mosquitoes feeding on *Habenaria obtusata* from the numbers carrying the pollinia of this orchid (Plate I, fig. 1). Further data have been obtained on this interesting association, and all the information now available is summarized in fig. 1. The numbers of left and right pollinia picked up are almost equal; Herschel (1883) reported a right-handed approach by bumble bees robbing *Salvia*. The process of picking up pollinia was observed in 1951; this was always at sundown; the mosquito appears to be greatly disturbed by the adherence of the pollinium; vigorous movements of the front legs, apparently directed at removing the encumbrance, are made as soon as the head is removed from the flower. The similar *Habenaria hyperborea* is visited by mosquitoes, but its pollinia have not been found on them. Darwin (1882) stated that this species is self-fertilized.

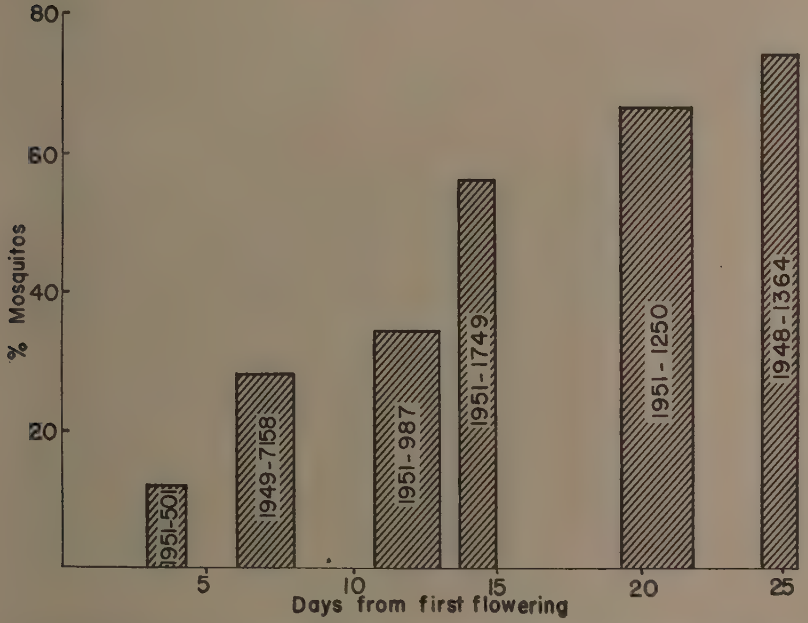


FIG. 1.—The progressive increase in the percentage of female mosquitoes which have visited *Habenaria*. Figures indicate year of observation and number of specimens examined.

Although there has been much controversy on this point, it is now generally agreed that mosquitoes feeding on sugar solution pass most of this to the oesophageal diverticula (*Aëdes aegypti*, Bishop and Gilchrist, 1946; *Anopheles* spp., Denisova, 1943; *Aëdes*, *Anopheles* and *Culex*, Trembley, 1952). This was confirmed for these northern *Aëdes* and for the black flies and tabanids by feeding dyed syrups (cf. de Boissezon, 1930), which could usually be seen in the crop through the body wall, and were always found there on dissection. After 3 to 4 hours there was some staining of the mesenteron. The following stains were tried ; the figures in brackets indicate the relative frequency with which each was found in the crop ; eosin (8), orange G (3), congo red (1), methylene blue (0).

There is very little information on the capacity of mosquitoes for nectar ; Nielsen and Greve (1950) found an average of 0·1 mg. of sugars in each of 4 specimens of *Aëdes cantans*. Stage and Yates (1936) reported *Aëdes vexans* and *Aëdes lateralis* taking blood meals equal to 115 and 143 per cent. of their unfed weights respectively. Hocking (1952*b*) found an average minimum weight of blood meal in northern *Aëdes* of 2·5 mg. In investigating the capacity of the crop, the air bubbles discussed by Macgregor (1930) and Marshall and Staley (1932) raised difficulties. The latter authors stated that these are displaced "more or less completely" when feeding on liquids other than blood. In these species they were never completely displaced, so that the full capacity of the crop is apparently not used.

In the crops of tabanids and simuliids there are no air bubbles. There is a single ventral diverticulum. In the different species this shows varying degrees of subdivision into two lobes. There are no data on the capacity of the crop. A few measurements of the size of blood meals have been made ; Cameron (1926) estimated that *T. septentrionalis* became engorged with 0·2 c.c. of blood ; Miller (1951) found *T. affinis* taking 108 per cent. of its unfed weight, and *T. septentrionalis* only 47 per cent.

Much information exists on the amount of nectar carried by the honey bee (Anon., 1927 ; Phillips, 1930 ; Root, 1940 ; Hammer, 1949), but most of this deals with average amounts carried rather than average capacity. Hüsing (1933), however, gave 0·075 c.c. as a maximum figure ; Bailey (1952) fed bees 0·04 c.c. of solutions in his study of the action of the proventriculus. For a long time it was generally held that the honey bee concentrated nectar by getting rid of free water on its way back to the hive (e.g., Getaz, 1905). Park (1932) clearly established that the only change that takes place at this time is a slight dilution occasioned by the addition of salivary secretions. Vansell *et al.* (1942) showed that nectar concentration influences bee activity. Butler (1945) found that the concentration and availability of nectar decided which plant species was preferred, while nectar abundance determined the number of bees visiting these flowers.

No measurements of the ingestion capacity of *Drosophila spp.* are known, but presumably some of the amounts fed by Wigglesworth (1949) are close to the maximum.

Some interesting information is available on the energy reserves of a few other species of insects and other animals. Grosch (1951) described an expansible crop acting as a food reservoir in *Habrobracon* ; he measured the size of this by feeding syrup, and found that it was correlated with the size of the individual. Beall (1948) studied the fat content of *Danaus plexippus* L. in relation to migration. Fulton and Romney (1940) and Cook (1944) have done similar work on the leafhopper *Eutettix*. This work shows an inverse correlation of distance travelled with fat reserves, and thus suggests that these insects are able to mobilize and utilize fat stores in flight. Kendeigh (1949) suggested that the migration of birds is dependent on seasonal changes in the energy resources. Greene (1919) showed a reduction in the fat content of the salmon from 15 to 2 per cent. during migration.

(b) *Experimental.*—In studying the food capacity of the adult insect, specimens were caught in the field, chloroformed, weighed and dissected in normal saline to expose the crop. Particularly when well filled with nectar, the crop could readily be removed whole and, if it was cut away close to the oesophagus, the tube constricted and prevented any loss of the fluid contents even when the sac was fully distended. The crop was then transferred to a waxed slide, a small incision was made in the upper surface through which the tip of a wax lined micro-pipette was inserted and the fluid withdrawn. The volume was read off, and the sugar content measured with a refractometer. If some leakage occurred at this stage it could readily be picked up without loss from the surface of the waxed slide. The crop of the mosquito is impermeable to water (Denisova, 1943), so that loss by evaporation prior to making an incision could be disregarded.

The pipettes used were wax lined as described by Wigglesworth (1937). Those used at first were made by drawing out capillary tubing to a fine tip ; the constriction of the bore proved a serious drawback with the more viscous solutions and in estimating quantities approaching the lower limit of the pipette. Later, pipettes were made from the stems of broken thermometers, ground to a point at one end. The permanent markings, the flattened uniform bore and the better adherence of wax to the ground tip proved decided advantages. Half-ounce rubber bulbs were used for suction. Pipettes were calibrated by weighing the mercury which filled a known length of the bore. Three sizes were used ; the total capacities were 0·07, 0·009 and 0·0026 c.c., and the the scale divisions represented 5·0, 0·056 and 0·0106 mm.^{3} approximately. They were recalibrated each time they were relined, but the changes were very small. At the higher concentrations the viscosity of solutions gave a good indication of the sugar content. For those over 70 per cent. it was necessary to apply suction by mouth ; the liquids were too viscous to be drawn into the fine capillaries with a rubber bulb. Viscosity may be the factor which limits the concentration of solutions ingested by mosquitoes. The quantities of fluid found in the crops were very variable, and rarely approached the maximum values obtained by the method which follows. These specimens gave the data on the maximum concentration of sugar solution found in the crop in nature (Table III, column 2).

To obtain maximum capacities, other field-caught specimens in batches of from 10 to 20 were enclosed overnight in petri dishes containing a layer of filter-paper soaked in 25 per cent. sugar solution. When thus held in close proximity to the food many specimens engorged fully ; the closer and more crowded the confinement, the more successful this was. The specimens which appeared fully fed were selected, and their ability to fly with their meals was confirmed. They were then chloroformed and treated in the same way as the field-caught specimens. The data obtained are given in full in Appendix A, and are summarized in Table III. Only those in which the crop still appeared full when it was exposed (marked * in Appendix A) were used in calculating the mean crop capacity. The figures on the mean empty weight of the insect, obtained by subtracting the weight of the crop contents from the initial weight, have already been presented in Table I.

Table III.—*A summary of the data on crop capacities, the concentrations of sugar solutions found therein, and the total energy resources of the adult insects.*

Species.	Mean capacity of crop (mm.^{3}).	Maximum percentage of sugars in crop contents.	Mean full load as percentage of basic weight.	Reserves in tissues and crop expressed as glucose (mg.).	Mean total energy in tissues and crop (erg × 10^8).	
					(per insect).	(per mg. basic weight).
Tabanus affinis	66·1±26·1 (10)	76	64	71·7	112	0·79
T. septentrionalis	32·9±18·5 (7)	75	84	35·6	55·5	1·02
Chrysops furcata	7·20±2·4 (8)	68	42	7·09	11·1	0·49
C. nigripes	7·23±2·1 (10)	67	51	6·88	10·7	0·57
Aëdes campestris	3·17±0·64 (9)	62	79	2·82	4·41	0·84
A. communis	0·91±0·23 (11)	42	45	0·582	0·91	0·38
A. nearcticus	1·83±0·24 (10)	58	96	1·484	2·32	0·95
A. punctor	3·39±0·82 (10)	55	95	2·575	4·02	0·90
Simulium venustum	2·16±0·81 (9)	76	124	2·284	3·57	1·48
S. vittatum	1·52±0·29 (10)	60	103	1·231	1·92	0·99
Apis	50·3±12·2 (10)	34*	78	42·2	66·0	0·79
Drosophila	0·172±0·057 (7)	24*	40	0·207	0·324	0·59

* All specimens laboratory fed on 25 per cent. sugar solutions. For purposes of comparison subsequent figures assume, arbitrarily, 60 per cent. to be the maximum available in the field.

An attempt was made to obtain similar readings on the paired dorsal diverticula of the mosquitoes. These peculiar structures are much more difficult to remove than the ventral diverticulum, and their contents leak out more readily. Their combined capacity in every species examined amounted to rather less than a quarter of that of the crop; they invariably contained air-bubbles, usually a greater proportion of them than the ventral structure, so that their actual content of sugar solution was probably never more than 10 per cent. of the capacity of the crop. Even from specimens of the large *Aëdes excrucians* Wlk. which had been enclosed with 25 per cent. sugar solution, no samples measurable with a pipette could be obtained from the dorsal diverticula.

During these studies specimens of both *T. affinis* and *S. venustum* were found in which the ventral diverticulum was ruptured, apparently by excessive feeding on the sugar solution, which was found free in the body cavity. Such specimens were always dead or nearly so; they were the only specimens which proved incapable of flight. The greatest crop load with which any specimen flew was 217 per cent. of the basic weight (*S. venustum*).

The same technique was used to study the capacity of the bee and *Drosophila*, but it was less satisfactory with these insects. This was because of the different structure of the bee's crop, and the small size of *Drosophila*. It was necessary to pool several samples from *Drosophila* to obtain a reading of the sugar content.

The greatest additional weight lifted given by Plateau (1865) is 184 per cent. of the body weight for *Syrphus corollae*; his mean figure for the bee is 78 per cent. Presumably the body weight which he used was the average fed weight. Schmidt (1939), by the ingenious procedure of attaching living insects to the top of hydrometers of suitable size, found the bee capable of lifting itself plus an additional 75 per cent. of the body weight. These figures are in such good agreement with those in Table III, column 4, that it seems that the load which these insects can carry is limited mutually by the capacity of the crop and the thrust which can be exerted by the wings.

(c) *Field observations.*—No special study was made of the flower visits of biting flies, observations made during other studies are given in Table IV. Conspicuous among other flower visitors were *Bremus frigidus* Sm. and *B. sylvicola* Kby., syrphid and calliphorid flies, ants, and the muscid fly *Lasiopssub rostatus* Zett. which was very abundant on *Dryas integrifolia*.

TABLE IV.—*Visits to flowers by biting flies recorded at Churchill, Manitoba, 1948–52.*

Insect species.	Plant species.	Date.
TABANIDAE :		
Tabanus affinis	**Ledum groenlandicum* *Ledum palustre* **Salix sp.*	1949, 1951, 1952
T. septentrionalis	**Ledum groenlandicum*	1949, 1951, 1952
	**Ledum palustre*	
	Heracleum maximum	29.vii.51
T. metabola McD.	**Dryas integrifolia*	21.vii.48
Chrysops mitis O.S.	*Solidago sp.*	28.vii.48
CULICIDAE :		
Aëdes nearcticus	*Rubus Chamaemorus*	24.vi.51
A. punctor	*Habenaria hyperborea*	15.vii.48
Aëdes sp.	*Achillea Millefolium*	20.vii.51
Aëdes sp. ♂	*Rubus Chamaemorus*	24.vi.51
Aëdes all spp.	**Habenaria obtusata*	Throughout flowering period
SIMULIIDAE :		
Eusimulium furculatum Shewell (♂ and ♀)	*Salix cordifolia* ♂ and ♀	28.vi.51
	Rubus acaulis	29.vi.51
Simulium venustum	*Cicuta Mackenzieana*	4.viii.51
	Heracleum maximum	26.vii.51
(♂ and ♀)	*Achillea Millefolium*	29.vii.51
	Rubus acaulis	29.vi.51

* Based on pollen grains collected from the insects; other records by direct observation.

All records females except where indicated.

Specimens of *A. punctor*, *S. venustum* and *S. vittatum*, the species which gave the highest load figures experimentally, were collected heavily engorged with nectar in the field, in most interesting circumstances. On more than one occasion swarming flights of females of these species were observed. There appears to be only one previous report of swarms of female mosquitoes (Howard *et al.*, 1912, p. 126, citing Goeldi) apparently of different significance, but Snyder (1917) has described what may have been something similar in *Tabanus americanus* in Florida, and J. A. Downes tells me that he has seen a swarm of females of a species of *Culicoides*. The fact that Kennedy's (1939) observations on the visual responses of mosquitoes were made on females, indicates that this sex might be expected to form swarms under suitable conditions.

The swarms of *A. punctor* are such striking phenomena as to warrant detailed description. Observations were made on two swarms in 1951 and two in 1952; mosquitoes were much less abundant in the latter year, and the swarms were smaller. The positions and shapes of the swarms are shown in Plate I, fig. 2: it is clear from their proximity to the boundaries between light and dark areas that visual stimuli play a part in their formation. Both of the 1952 swarms developed over the only tent in which heating was on at the time, so that temperature gradients also appear to be important. All except one of the swarms developed shortly before sunset and persisted for about an hour, by which time there was not enough light for observations on the break-up of the swarm. The exception, the earlier swarm in 1952, developed at about 02.00 hrs. and extended not only over, but also inside the tent. The noise it made was intense enough to awaken the writer and prompt these observations. It dispersed when light rain started at 02.30 hrs. Times, dates, meteorological data and the weights of mosquitoes and the contents of their crops are summarized in Table V. Mosquitoes composing the swarms showed no interest in obtaining blood meals—a strange parallel with the reluctance of swarming bees to sting. This was not due to unfavourable weather, as quite high biting rates were sometimes recorded just before and also just after the swarms. The distension of the abdomen by nectar could readily be seen in specimens on the wing, and resulted in the drooping of this part of the body. The movements of individuals were much the same as those of male mosquitoes in mating swarms, on a bigger and more intense scale, giving an impression of boiling. The larger, 1951, swarms each contained an estimated half a million mosquitoes. Half a pound of specimens was collected from one of them in ten minutes with a 12-in. net without appreciably diminishing its extent.

The swarms of the two black-fly species were much less striking: smaller, less well defined, and with less intense activity. The 1951 swarm of *S. vittatum* formed over the head of an entomologist, than which it was a little larger, and accompanied him as he walked along a railway track. The 1952 swarm formed over a pile of fishplates by the same railway track. There was no conspicuous object under the swarm of *S. venustum*. Both species showed a similar distension with nectar and lack of interest in blood meals. All specimens examined from swarms, both mosquitoes and black flies, had been fertilized.

The intense aggregation, the lack of interest in blood meals, the time of day and the quantities of nectar carried, all suggest that these events represent the prelude to migratory flights, the probable distance and duration of which is discussed in Part V.

It is clear from these observations that the capacities measured under artificial laboratory conditions (Table III) are not unrelated to the quantities of

Table V.—*Meteorological conditions at the time of the formation of female swarms of biting flies and the quantities of sugars found in participating insects.*

Species and date.	Temp. (° F.)	Wind (direction and speed).	Barometer (inches Hg.).	R.H. (%).	Mean weight of sugars per specimen (mg.).
Aëdes punctor					
25.vi.51	56	E.S.E. 8	29·65 falling slowly	67	1·04
29.vi.51	44	W.N.W. 5	29·76 falling slowly	93	0·93
22.vi.52	48	Calm	29·64 steady	92	.
24.vi.52	54	.	29·88 falling slowly	87	0·84
Simulium venustum					
8.vii.52	58	W.N.W. 4	29·76 steady	.	0·86
S. vittatum					
25.vi.51	64	.	.	49	.
28.vi.52	61	S.S.W. 6	30·08 steady	56	0·74

food actually carried in nature. All species could carry more reserves in the crop than in the tissues, the ratio of the two ranging from 2·75 for *Drosophila* to 96 for *S. venustum.*

3. Nectar Supply and Demand in the Sub-Arctic.

Little scientific interest has been taken in the secretion of nectar by plants. Most studies have been commercially inspired and have been conducted in relation to honey production. Plant physiologists and entomologists alike have been content to leave this field, of importance to both of these groups, in the hands of the apiculturist.

It is not generally realized what a large proportion of adult insects are almost entirely dependent on this plant secretion. These include probably most of the Diptera, Hymenoptera, and Lepidoptera, a considerable number of Coleoptera, and a few smaller groups from several other orders. Nectar must have tremendous significance in the dispersal of these species.

(a) *Review.*—As Lovell (1950) pointed out, almost any part of a flower may secrete nectar, although nectaries are commonly associated with the generative organs. Kerner (1902) stated that the dehiscence of the stamens usually faces the source of nectar, and gave an excellent review of the information available at that time on nectaries and flower pollination. Bonnier (1879) made a thorough study of the structure of nectaries and many contributions to their physiology; he anticipated some of the findings of later workers. Andreev (1928) claimed that in a given inflorescence the nectaries are smaller in the higher flowers, and that there is a corresponding gradient in the quantity of nectar secreted. Jaeger (1950) claimed that axial nectaries have tended to replace those associated with stamens or carpels in the Dicotyledons, and suggested that their position has phylogenetic significance.

The mechanism of nectar secretion is a problem in cellular physiology to which no complete solution is yet possible. Trelease (1920) discussed the cellular structure of nectaries, and considered that vigorous growth favours nectar production. Steel (1924) found that nectar which was not removed was reabsorbed by a flower, apparently going to nourish the ovary, which he suggested was the original purpose of nectar. Percival (1946) made a careful study of flowering and nectar secretion in *Rubus fruticosus* and found that secretion followed the growth rhythm of the plant, with a diurnal rhythm superimposed on this. A contribution to the understanding of the passage of sugars through the cell membrane has been made by Arens (1949).

Four methods have been used to obtain nectar samples from flowers. The simplest is removal with a micro-pipette, although some practice is needed to secure accurate results, and it may necessitate destruction of the flower. Water extraction may permit more accurate measurement of the total sugars present, but does not allow measurement of either volume or concentration. A centrifuge method was described by Ewert (1932) and refined by Swanson and Shuel (1950), who found it faster and more reliable than either micro-pipette or water extraction. Finally, Park (1932) established the reliability of the method first used by Bonnier (1879), employing the honey bee as a convenient intermediary. He measured the small and constant dilution of nectar which takes place in the crop. This only permits concentration to be measured.

When nectar samples have been obtained the sugar content may be investigated chemically ; optically, with a refractometer or a polarimeter ; or physico-chemically using paper partition chromatography (Partridge, 1948 ; Wykes, 1952). Since adequate quantities for polarimeter studies are rarely available, chemical or chromatographic analysis is usually necessary if information on the sugars present is required. Most nectar feeders have enzymes which permit utilization of all the important sugars present (e.g., Wigglesworth, 1931 ; Phillips, 1927 ; Hassett, 1948 ; Oertel *et al.*, 1951). The nature of the sugars is thus not important when only energy values of nectars are required, and measurements of the refractive index are sufficient. Park (1929*a*, 1932) found the refractometer more accurate than micro-chemical methods.

There have been many studies of the factors which influence the amount and concentration of nectar secreted. The commonest finding is an inverse correlation between concentration and relative humidity (Kenoyer, 1917 ; Park, 1928*b*, 1929*b* ; Beutler, 1930 ; Vansell, 1940 ; Scullen, 1940, 1942 ; Oertel, 1946), although often this would have been more correctly expressed as a direct correlation between concentration and saturation deficiency, or an inverse correlation with vapour pressure. Shuel (1952) attributed this mainly to direct hygroscopic changes. Park (1928*b*) found that concentration tended to vary inversely with amount. Most workers have found that high temperatures favour an increase in either amount or concentration (Trelease, 1920 ; Demuth, 1923 ; Vansell, 1940 ; Sistek, 1940 ; Oertel, 1946), or in both (Hammer, 1949). Others (Kenoyer, 1917 ; Mitchener, 1927, 1951 ; McLachlan, 1933), found the daily range of temperature to be important ; if this is correct, bee-keeping should be more productive in areas with a continental than in those with a maritime climate ; there is no evidence that this is so. Getaz (1905) considered that each plant species had an optimum temperature for secretion ; Beutler (1930) could find no effect attributable to temperature.

An increased secretion with greater irradiation or a decreased secretion in darkness was shown by Kenoyer (1917), Mitchener (1927), Beutler (1930), Roswall (1950) and Shuel (1952). Park (1930*a*) and Vansell (1943, 1944*a*) found varietal differences in nectar secretion in *Gladiolus* and in alfalfa and cotton respectively ; Shuel (1952), however, stated that, in red clover, environmental factors are more important than heredity, but added that selection for high-yielding strains may be possible. The influence of fertilizers has been considered by Sistek (1938) ; Getaz (1905) regarded limestone areas as favourable for nectar secretion ; Stapel and Götzsche (1941) found that secretion was reduced by potash fertilizers.

Other factors which have been reported to affect nectar secretion include age of flower (Kenoyer, 1917 ; Beutler, 1930 ; Pankratova, 1950), time of day and position of flower or floret (Park, 1930*b*), insecticide applications (MacVicar *et al.*, 1952), frequent removal of nectar (Wykes, 1950, 1951), fertilization (Stapel and Lund, 1945), altitude (Lunder and Lunder, 1946), latitude (Bonnier, 1879 ; Roswall, 1950), and thunderstorms (McLachlan, 1933). Beutler (1930) found that soil moisture had little or no effect, and Percival (1946) found no obvious effects from weather conditions. Shuel (*in litt.*, 1952) considers insolation to be the dominating factor. Some of the more important information published on the concentration and quantity of nectar secreted by plants is summarized in Table VI.

TABLE VI.—*A summary of published information on the concentration and amount of nectar secreted by flowers.*

Plant species.	Per cent. sugars.	Amount mg. total sugars/flower.†	Author.
LILIACEAE :			
Fritillaria	2·5	.	Bonnier, 1879
imperialis	9·4	.	Wykes, 1952
IRIDACEAE :			
Gladiolus primulinus	26·6–30·7	.	Park, 1932
SALICACEAE :			
Salix spp.	60	.	Vansell, 1939
PROTEACEAE :			
Protea mellifera	17·66	.	von Planta, 1886
PORTULACACEAE :			
Claytonia almoides	.	0·413	Wilson, 1878
CARYOPHYLLACEAE :			
Stellaria sp.	50	.	Chabot, 1948
RANUNCULACEAE :			
Aconitum Napellus	.	6·41	Wilson, 1878
Delphinium sp.	*71	.	Braun, 1950
MAGNOLIACEAE :			
Liriodendron Tulipifera	14·4–36·4	296	Marvin, 1933
CAPPARIDACEAE :			
Cleome lutea	23	abundant	Pellett, 1940
CRUCIFERAE :			
Brassica sp.	50	.	Chabot, 1948

TABLE VI.—*A summary of published information on the concentration and amount of nectar secreted by flowers*—(continued).

Plant species.	Per cent. sugars.	Amount mg. total sugars/flower.†	Author.
ROSACEAE:			
Malus baccata	.	0·43	Beutler, 1930
M. sylvestris	1–70	.	Keitt and Ivanoff, 1941
Prunus Cerasus	29	.	Hammer, 1949*b*
Pyrus communis	3–45	.	Keitt and Ivanoff, 1941
Rubus idaeus	.	24·92	Beutler and Schöntag, 1940
Rubus sp.	34–35·6	.	Chabot, 1948
LEGUMINOSEAE:			
Lathyrus latifolius	.	9·93	Wilson, 1878
Medicago sativa	20–35	.	Hammer, 1949*a*
	22–67	.	Vansell, 1943
	.	0·88	,, ,,
Onobrychis sativa	.	0·2	von Planta, 1886
O. viciifolia	23	.	Caillas, 1947
Robinia viscosa	.	0·5	von Planta, 1886
Trifolium pratense	*57, 44	.	Hammer, 1949*a*
	.	6·2 (head)	Kenoyer, 1917
	.	7·93 (head)	Wilson, 1878
T. repens	29·8–55·1	.	Scullen, 1942
	40·1	.	Chabot, 1948
	.	5·8 (head)	Kenoyer, 1917
Trifolium sp.	33·3–47·7	.	Vansell, 1939
Vicia sp.	22–57	.	,, ,,
	.	3·16 (head)	Wilson, 1878
RUTACEAE:			
Citrus aurantium	28	*0·6	Caillas, 1926
	19·8–25·75	5·1	Vansell *et al.*, 1942
Aesculus hippocastaneum	*79·7	.	Beutler, 1930
VITACEAE:			
Vitis sp.	65·75	.	Chabot, 1948
MALVACEAE:			
Gossypium sp.	19–28	10·3	Vansell, 1944*a*
	16–36	.	,, 1944*b*
ONAGRACEAE:			
Epilobium angustifolium	35·5	.	Chabot, 1948
	28·5–65·5	.	Scullen, 1942
Fuchsia sp.	.	7·59	Wilson, 1878
UMBELLIFERAE:			
Daucus Carota	32·5–46	.	Hammer, 1949*a*
ERICACEAE:			
Calluna vulgaris	43–63·8	.	Lunder and Lunder, 1946
Rhododendron hirsutum	.	0·47	von Planta, 1886
OLEACEAE:			
Syringa sp.	*71.	.	Braun, 1950
ASCLEPIADACEAE:			
Asclepias cornubi	.	1·86	Beutler, 1930
A. syriaca	16–64	.	Park, 1929*a*
Hoya carnosa	40·77	.	von Planta, 1886
LABIATAE:			
Lavandula vera	15·5	.	Bonnier, 1879

Table VI.—*A summary of published information on the concentration and amount of nectar secreted by flowers*—(continued).

Plant species.	Per cent. sugars.	Amount mg. total sugars/flower.†	Author.
BIGNONIACEAE :			
Campsis radicans	27–38	.	Park, 1929*a*
	15.3	.	von Planta, 1886
CAPRIFOLIACEAE :			
Lonicera Periclymenum	21	.	Bonnier, 1879
COMPOSITAE :			
Taraxacum officinale	.	92 (head)	Kenoyer, 1917
Taraxacum sp.	51·2	.	Vansell, 1939
GENERAL :			
17 spp., Germany	8–70, 40	.	Beutler, 1930
Many spp., Germany	7–76·6	mostly 1–2	Beutler and Schöntag, 1940
Unspecified	5–75	.	Pryce-Jones, 1950
,,	9·05–41·2	.	Steel, 1924.
76 spp. U.S.A.	4–65	.	Vansell, 1939
66 spp. Israel	12–87	.	Fahn, 1948
Numerous spp.	40–55	.	Park, 1928*b*
41 spp., Quebec	20–65·75	.	Chabot, 1948
57 spp., Germany	9–76	0·02–7·6	Beutler, 1949

* Maximum value ; single figures are averages unless so marked.

† Approximations, where author expressed his results in other terms. Figures are amount secreted in 24 hours except those of Marvin (the life of the flower) and Wilson, Kenoyer, and Vansell (time unspecified).

The competition between insects for the available nectar and the competition between plants for the services of pollinating insects have been discussed by several authors (Clements and Long, 1923 ; Vansell, 1943 ; Grant, 1950), and have an important bearing on this study. Further discussion is unlikely to be profitable until more is known of insect populations and nectar production on an area basis. Stapel and Lund (1945) are the only authors who have given figures for nectar production per unit area, and their figures are only for cultivated plants. Wedmore (1932) gave figures for honey yield per acre of various crops, but these are largely conjectural.

(b) *Experimental.*—Preliminary observations in the Churchill area on flowers not protected from the visits of insects showed little or no nectar in any but highly specialized flowers such as *Arctostaphylos* and *Andromeda.* This suggests that under normal conditions there is, as would be expected, an even balance between supply and demand. To determine the concentrations and quantities of sugar solutions available to biting flies in this area, it was therefore necessary to protect flowers from the visits of insects. At ground level this was done by covering them with glass lamp chimneys, one end pressed into the ground around the base of the plant, and the other covered with muslin. On shrubs and taller plants, flowers or inflorescences were covered with muslin bags closed around the stems with rubber bands. Protection was usually for 24 hours ; it was assumed that nectar present at the end of this time was secreted during the period of protection. Flowers were returned to the laboratory in closed containers, the nectar was removed and measured with a wax-lined pipette of the type already described (Part II, section 2(*b*)), at a magnification of 10 diameters. Sugar content was measured with a pocket refractometer reading directly in per cent. sugars by 1 per cent. divisions up to 50 per cent. Nectars containing over 50 per cent. of sugar were mixed with an equal volume of distilled water on the refractometer plate and the reading was corrected for the density difference. Thrips and other very small insects were often found in the flowers ; but no differences were found in the readings from flowers with and without these minor visitors. Occasionally ants were found either in the flowers or in the protective coverings ; when they were present there was never a measurable amount of nectar. Nearly 500 readings were taken on 93 plant species, the results are abbreviated in Appendix B, the plants arranged according to Gray (Fernald, 1950), and summarized in Tables VII and VIII, and fig. 2. Plate I, fig. 3, and Plates II and III illustrate some of the more important nectar-bearing plants.

TABLE VII.—*The total production of nectar in forest and on tundra, Churchill, Manitoba,* 1951 *and* 1952.

Species.	Mean percentage sugars.	Mean sugars/acre/day (mg.).	Duration of flowering period (days).	Total production (gm./acre/season).
TUNDRA :				
Salix arctophila	48	7515	31	233
Rhododendron lapponicum	67	7250	22	160
Salix planifolia	40	4680	24	112
Dryas integrifolia	27	1550	28	43
**Oxytropis campestris*	38	773	30	23
Vaccinium uliginosum	18	684	28	19
†*Arctostaphylos rubra*	29	403	30	12
Senecio congestus	28	318	26	8
Arnica attenuata	35	224	23	5
Salix reticulata	17	216	21	5
S. Richardsonii	27	156	26	4
Tundra average	50		Tundra total	624
FOREST :				
Ledum groenlandicum	47	3413	23	79
L. palustre	46	1220	29	35
Epilobium angustifolium	42	1858	19	35
Salix cordifolia	23	425	28	12
**Castilleja Raupii*	28	290	32	9
Salix candida	15	150	31	5
†*Ribes oxyacanthoides*	31	209	15	3
Potentilla palustris	12	118	15	2
Rubus acaulis	25	60	31	2
Forest average	42		Forest total	182

* Nectar not accessible to any of the biting flies without injury to the flower.
† Nectar not accessible to black flies or tabanids without injury to the flower.

TABLE VIII.—*Plant species secreting nectar containing over 70 per cent. of sugars, or producing over 0·01 c.c. of nectar per flower daily. Churchill, Manitoba,* 1951 *and* 1952.

Maximum concentrations % sugars.	
Epilobium angustifolium	77
Ledum groenlandicum	77
Rhododendron lapponicum	76
Parnassia palustris	75
Rubus acaulis	74
Ribes oxyacanthoides	72

Maximum volumes, c.c./flower/day.	
Potentilla palustris	0·053
Salix cordifolia	0·028
S. candida	0·018
S. arctophila	0·012
Epilobium latifolium	0·01

Readings of sugar concentration could be obtained with less than 1 mm.^{3} of liquid; even so, for some species composite samples from several flowers were necessary before a reading could be taken. Measurements of volume were made on single flowers except for the willows, clovers, and Compositae; the units used for these were the ament, raceme, and flower-head respectively. The quantities of sugar per flower unit per day were calculated for each concentration reading by multiplying this by the mean volume, and by the density of a sucrose solution of the same concentration. Densities were taken from international critical tables. The figures in column 6 of Appendix B are the averages for all concentration readings obtained on that day. The productivity in mg./acre/day (Appendix B, column 7; and Table VII, column 3) was obtained by multiplying the mean daily yield per flower by a factor based on the estimated abundance of the flower unit. The system of classifying plant abundance was adapted from Braun-Blanquet (1932), and the factors used were: dominant 8000, abundant 400, frequent 20, occasional 1, rare 0. For hyper-disperse plants the factors used were fractions of these equivalent to the estimated fractions of the terrain over which the plants occurred.

The nectar production on tundra is about 3½ times that in the forest. The forest in the vicinity of Churchill is very open. Most of the plant species examined from the forest were found in glades and clearings, burnt-off areas, or around the margins of streams, lakes and swamps. The differences in nectar production between tundra and typical coniferous forest would be much more pronounced. Also, the forest species of mosquito are produced in much larger numbers per unit area than the tundra species, so that a smaller supply of nectar, as far as mosquitoes are concerned, has to serve for a larger insect population. The other groups of biting flies cannot be clearly subdivided into forest and tundra species.

Two principal factors account for the lower nectar production in the forest: firstly, the dominant plants are coniferous trees which do not produce nectar; secondly, these trees screen the plants growing below them from the insolation upon which nectar secretion is so largely dependent. If it is assumed that the forest species of mosquito are produced in three times the numbers of the tundra species, then, given equal competition, in typical forest this factor alone might be expected to restrict them to one-fifteenth of the range of their tundra relatives.

The quantities and concentrations of nectar produced on tundra are adequate to permit large populations of biting flies to make full use of their energy carrying capacities. Fig. 2 shows that the peaks of nectar production on the tundra and in the forest are synchronous with the peaks of flight activity of the tundra and forest species of mosquito respectively. These data were compiled over several seasons ; the dates have been adjusted to count from the day of break-up of river ice as zero. The mosquito curve represents flight activity and is redrawn from Hocking *et al.*, 1950.

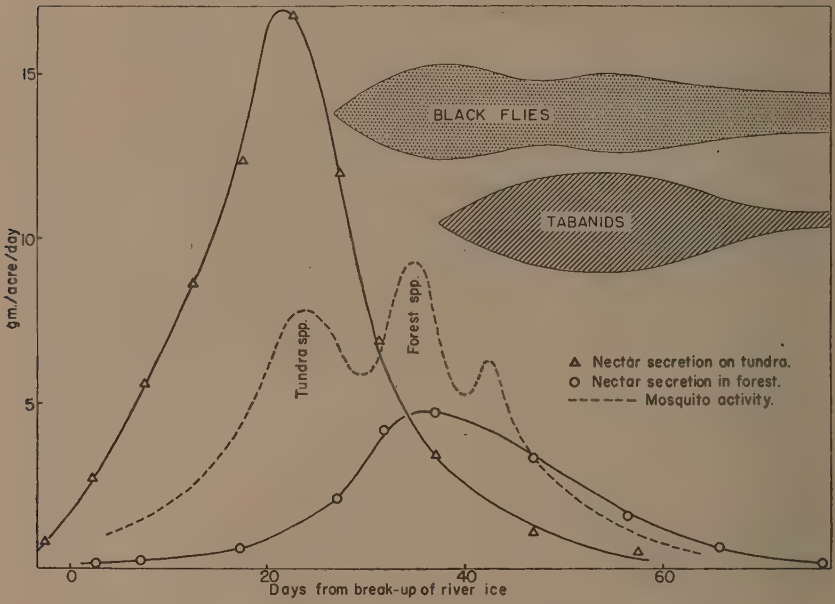


Fig. 2.—The seasonal changes in nectar production and biting fly populations, Churchill, Manitoba, 1947–1952.

There are no comparable figures for nectar production at lower latitudes, but a consideration of normal honey yields further south suggests that these northern figures are high. On tundra, sugar equivalent to 12,000 lb. of honey is produced within range of a single apiary site per season. The high concentrations also suggest that the total yield is high ; there are few previous records of nectars containing over 70 per cent. of sugar, and only one over 80 per cent. is known (Fahn, 1938). Average atmospheric saturation deficiencies at Churchill are very low, resulting in a tendency to low concentration readings. The length of day and, according to Bonnier, the latitude on its own account, would both tend to result in a high yield.

4. GENERALIZATIONS ON THE ENERGY AVAILABLE.

The mean full load (Table III) rather than the maximum full load (Appendix A) is regarded as the significant figure. This is because, firstly, migrations are normally made by large numbers of insects collectively rather than by single individuals; secondly, it normally requires more than the arrival of a single exhausted individual, even if this is a fertilized female, to establish a species in a new area. There is a tendency for the percentage of the basic weight which can be carried to decrease with increasing size; this is expected from the greater power per unit weight required to support the larger insect. Weight for weight, the energy value of fats is about three times that of an 80 per cent. sugar solution, so that insects which can utilize fats for flight could carry about three times as much energy for the same lifting ability. The extent to which advantage could be taken of this, however, may be curtailed by the necessity for carrying surplus water to provide for evaporative cooling in flight. The amount of energy available for flight which an insect using nectar may carry per mg. of basic body-weight may be provisionally set at $1{\cdot}5 \times 10^8$ ergs for the smallest insects, tending to zero for the largest.

Insects which utilize fats have less well-developed flight muscles, apparently never more than 25 per cent. of the body weight (Magnan and Perrilliat-Botonet, 1932). This limits the load they can carry, and the maximum fat content reported is not more than 35 per cent. of the weight—perhaps 50 per cent. of the basic weight (Fulton and Romney, 1940; Williams, 1945; Beall, 1948; Weis-Fogh, 1952*a*; Cheu, 1952). This is equivalent to about $2{\cdot}0 \times 10^8$ ergs per mg. basic weight, rather more than twice that which an insect of similar size might carry in the form of nectar.

PART III.—THE POWER OUTPUT REQUIRED FOR INSECT FLIGHT.

This is still a controversial subject. In becoming air-borne the work an insect does against gravity is equal to the product of its weight and the distance through which it rises. This work is converted to potential energy and is recoverable during a subsequent descent. It thus has little bearing on flight range except where high mountains must be crossed, most migratory flights being made quite close to the ground (Williams, 1930). For most purposes it is convenient to divide the power required for level flight into two parts—the power required for support and the power required for propulsion.

1. THE POWER TO REMAIN AIRBORNE.

(a) *Review.*—The more complex part of the work done is that required to support the insect in the air. It was early supposed that this should equal the rate at which gravity would do work on the insect, that is, it should depend on the limiting velocity of fall. Wellington (1945) measured the "vertical" wind resistance of some insects, which at the limiting velocity of fall would equal the weight. The power required for support might thus be calculated approximately from his data.

Fitzgerald (1910) showed that the power required to support a given weight varied inversely as the frequency of wing beat. Magnan (1934), and Magnan and Sainte-Laguë (1933) supposed that the insect falls freely during the up stroke of the wing, and that work is done during the down stroke equal to the kinetic energy acquired during the up stroke plus the work required to lift the insect back to its initial level. It has been shown however (Williams and Galambos, 1950; Osborne, 1951; Chadwick, 1953) that an insect may obtain lift during both the up and the down strokes of the wings. Indeed, in hovering flight the wings move backwards and forwards, rather than up and down (von Holst, 1948). In any event the velocity of fall at the end of the up stroke could not be accurately calculated even if the insect were to fall freely; it would depend on the wing area as well as on the frequency or time of fall.

Magnan (1934), and Osborne (1951), using Magnan's data, have calculated the power required in terms of the distances which the wings have to be moved against the forces due to air resistance. This procedure should give the power which must be put into the wings, which is equal to the product of that theoretically required for flight and the aerodynamic efficiency, discussed in the next section. The results Magnan obtained by this method led to his statement: "C'est ainsi qu'au point de vue de la sustentation et de la propulsion j'ai laissé de côté les lois de la résistance de l'air." Osborne's calculations led to a figure for power output of 10^{-2} h.p. per lb. of muscle ($1{\cdot}64 \times 10^5$ erg/gm./sec.). This is the same value as is often used for the maximum continuous output for man (e.g., Gawn, 1948; Parry, 1949), and is based on Henderson and Haggard's (1925) study of a Harvard rowing crew. Presumably these subjects were not average men, and certainly they were not in average training; the value used here for the maximum continuous output of the average man is $0{\cdot}61 \times 10^{-2}$ h.p./lb. of muscle, or 10^5 erg/gm./sec. Insects, on account of their smaller size, might be expected to do much better than this (Hill, 1950).

Hoff (1919*a*, *b*) applied Prandl's aerodynamic theory to the figures given by Demoll (1918) to derive a formula for lift in terms of the speed and wing area. He pointed out the similarity between the air flow through the vibrating wings of an insect and that through an actuator disc or aircraft propeller. This similarity has also been emphasized by Betts (1931) in an account of the flight of the honey bee, and shown experimentally by von Holst (1943, 1948). The Diptera and Hymenoptera at least may in fact be regarded as diminutive helicopters using two single-bladed, semi-rotary, reversible pitch rotors (e.g., Sotavalta, 1950). This suggests that the most reliable value for the work done in remaining airborne would be given by applying the momentum propeller theory of Froude (Bairstow, 1939), which is used in performance calculations on helicopters. This states that the thrust is equal to the momentum generated per second in the slipstream. For a hovering insect the thrust (T) would be vertical, and equal to the weight; for one in forward flight its vertical component would equal the weight, and its horizontal component the parasite drag. Thus:

$$T = Mg = mv, \text{ or } v = \frac{Mg}{m}, \quad . \quad . \quad . \quad . \quad (1)$$

where M is the mass of the insect, m the mass of air passing through the wings per second, and v the vertical component of the velocity imparted to this. The work done is equal to the vertical component of the kinetic energy generated in the slipstream, and the power required is the work done per second:

$$\text{K.E./sec.} = \frac{mv^2}{2} \text{ or from (1), } \frac{m}{2}(Mg/m)^2 = \frac{M^2g^2}{2m} \qquad (2)$$

It was thus necessary to measure experimentally the mass of air passing through the wings per second. This may be expected, in similar insects, to be proportional to the volume swept out by the wing in rotating as a flat plate about an axis through its base, in its plane and perpendicular to its length. That is, to the wing area and length, and the amplitude and frequency of wing beat, and since there are two wings and they move through twice the angular amplitude per cycle, this may be expressed as:

$$m = 4k\rho.Al\theta n, \qquad . \quad . \quad . \quad . \quad . \tag{3}$$

where A and l are the wing area and length, θ the amplitude in radians, n the frequency and ρ the density of air, and where k is a constant, the values of which would be similar, for related species. The term *wing action constant* is proposed for k. The density of air at *S.T.P.* is unsuitable for this study since few insects fly at 0° C. The value at 760 mm. and 60° F., (0·00122 gm./c.c.) is therefore used.

TABLE IX.—*The dimensions of wings and wing movements, the mass of air passing through the wings per second, and the power required to remain airborne.*

Species.	Wing area (cm.^{2}).	Wing length (cm.).	Max. amplitude in radians.		Frequency (cycles/sec.).		Mass of air (gm.).	Power to remain airborne (erg./sec.)
			Range.	Mean.	Range.	Mean.		
Tabanus affinis	0·574 ± 0·021	1·43 ± 0·02	2·04–2·86	2·39	96–143	119	.	.
	.	.	.	.	*110–133	122	.	.
	.	.	.	.	†108–149	127	2·275	4270
T. septentrionalis	0·293 ± 0·019	1·02 ± 0·03	1·87–2·91	2·74	58–128	98	0·759	1870
Chrysops furcata	0·219 ± 0·012	0·86 ± 0·03	1·97–2·93	2·53	98–157	110	0·496	510
C. nigripes	0·189 ± 0·010	0·81 ± 0·02	2·48–2·67	2·53	105–113	109	0·401	447
Aēdes campestris	0·064 ± 0·008	0·53 ± 0·02	1·22–1·71	1·90	311–332	322	0·197	66·5
A. communis	0·039 ± 0·003	0·44 ± 0·02	0·91–1·52	1·93	213–230	216	0·0680	41·6
A. nearcticus	0·036 ± 0·003	0·38 ± 0·01	1·88–2·06	1·98	305–380	318	0·0877	35·4
A. punctor	0·064 ± 0·007	0·53 ± 0·02	0·96–1·80	1·52	223–360	290	0·142	68·4
Simulium venustum	0·038 ± 0·004	0·32 ± 0·01	2·23–3·02	2·65	198–280	258	0·0790	35·1
S. vittatum	0·046 ± 0·005	0·33 ± 0·02	2·48–3·28	2·95	170–224	209	0·0886	20·6
Apis	0·283 ± 0·018	0·92 ± 0·02	2·02–2·82	2·18	178–208	198	.	.
	(fore + hind)	.	.	.	*200–206	204	1·06	3150
Drosophila	0·015 ± 0·001	0·214 ± 0·005	1·97–2·37	2·23	185–224	208	0·0141	10·3

* Measurements made by reflection method.
† Measurements made by stationary wave method.

(b) *Experimental.*—The mass of air passing through the wings was measured directly for *T. affinis* and the bee only. A, l, θ and n were measured for all species, and the value of k obtained from the data on *T. affinis* was used in calculating values of m for the other dipterous species.

Wing areas were measured by mounting the wings in euparal on slides, and making photographic prints from these by projection on high contrast paper at a magnification of 10 diameters. To guard against dimensional changes in the paper a portion of translucent millimeter scale was included. Areas and lengths were measured from these prints, the former with a planimeter. The fringes of scales along the anal margins of the wings of mosquitoes were included in the areas. Lengths were measured from the wing tip to the articulation of the radial vein with the pleural wing process. At least 20 specimens were measured for each species; the results are summarized in Table IX.

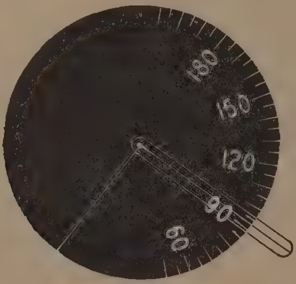


Fig. 3.—The instrument used to measure amplitude of wing beat.

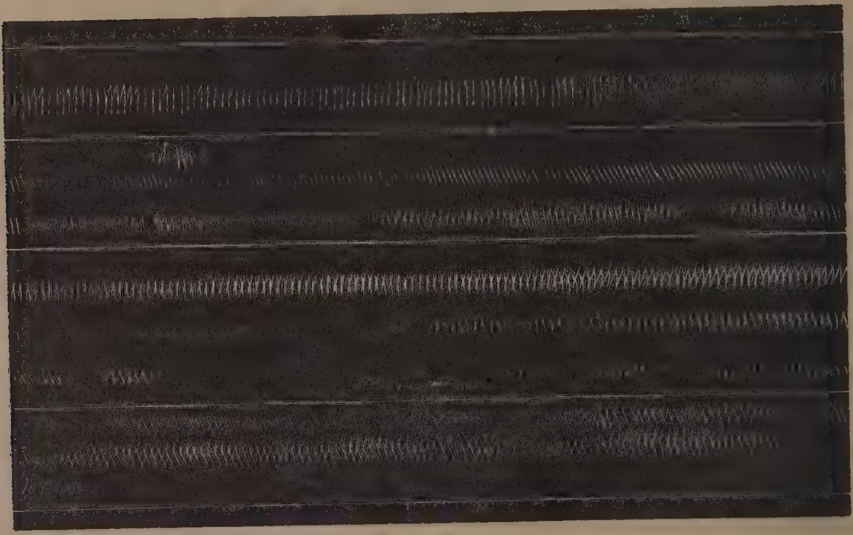


Fig. 4.—A portion of a kymograph tracing of wing-beat frequency. Top line, *T. septentrionalis*; Second line, *C. furcata*; Third line, *C. nigripes*; Bottom line, *C. carbonaria*.

To measure the amplitude of wing beat, insects were anaesthetized with cardon dioxide and mounted on the points of wedge-shaped pieces of aluminium foil with the help of the holder shown in Plate V, figs. 1 and 2. A 1 : 3 mixture of resin and beeswax was used for attaching *T. affinis* and the honey bee, a 1 : 4 mixture for the other species. A droplet of this was first melted on to the end of the strip of foil, and then on to the insect mesonotum. This was done with an electrically heated nichrome wire, the temperature of which could be controlled as described by Hollick (1940); gauge 30 wire was used for the smaller insects, gauge 24 for the larger. The area of the mesonotum covered with wax was kept as small as possible consistent with firm attachment. At intervals after recovery the insects were held in front of the instrument shown in fig. 3, so that the wing base was directly over the centre, and viewed against strong back lighting, while a current of air was directed against the head. They were inclined at such angles that the true amplitude could be seen, i.e., the actual angle through which the wing moved, and not the apparent amplitude as seen in a frontal view. The envelope of wing movement was clearly visible. The instrument was turned so that its base line was directly below one limit of the envelope, and the lever moved round until it was directly below the other limit. A magnification of 10 diameters was used for *Drosophila* and black flies. Several specimens were observed for each species, and the highest reading for each specimen was recorded.

Frequencies of wing beat were measured using insects mounted in the same manner, and allowing the wing tip to trace a path on smoked paper on a kymograph drum. A paper speed of 19·3 cm./sec. was used for all species, and a time trace marking seconds and one-fifth seconds. By using a light smoking and a very light contact, satisfactory traces were obtained in this way even with *Drosophila*. Insects were held so that the wing movement was in the plane of the axis of the drum. A portion of a typical tracing is reproduced as fig. 4; the lemniscate path is indicated in most of the traces. Frequency readings for *T. affinis* and the honey bee were also obtained by using a visual form of the photographic method of Hollick (1940). When the insects were flying on the mill used for measuring efficiency (Part IV), the successive strokes of the wing could be clearly seen when light was arranged to strike the insect from a suitable angle. By arranging a curved scale just behind the path of the insect, the distance travelled per wing beat could be measured to the nearest mm. on each revolution; dividing this distance into the known speed of flight gave the frequency. A further method, believed new, was also used with *T. affinis*. When the insect was suspended on a thread attached to the mesonotum (Part IV), and this was kept in tension in spite of flight movements by an additional load, the thread was observed to be thrown into stationary waves by the vibration of the thorax. The length of these waves was measured and the frequency calculated from the expression:

$$n = \frac{1}{2 \times \text{wavelength}} \sqrt{\frac{\text{Tension}}{\text{Mass per unit length.}}}$$

To measure m, the mass of air passed through the wings per second, a commercial air-flow meter of the hot thermopile type was used. This accepted a column of air $\frac{1}{2}$ in. in diameter and gave a directional reading. The insects were mounted on aluminium points, as for frequency and amplitude measurements, and were then clamped in their level flight positions at such a height that the receiver of the air-flow meter resting on the bench was just out of reach of the extended tarsi. The instrument was then adjusted parallel to the dominant direction of the slipstream, i.e., so as to give the maximum reading, and was moved over a $\frac{1}{4}$ in. square grid on the bench surface. The angle of inclination was recorded, and for each species the mean value of this agreed with the value obtained from the relative positions of the wings and the points of peak velocity in fig. 5. An air speed reading was taken at each point of the grid. With *T. affinis* it was possible to obtain two sets of readings, that is about 400 figures, for most specimens. Eight specimens were used. The highest single reading recorded was 330 cm./sec. Magnan and Magnan (1933) found slipstream speeds up to 800 cm./sec. using a hot wire anemometer. The honey bee proved much less satisfactory, and it was often necessary to use two

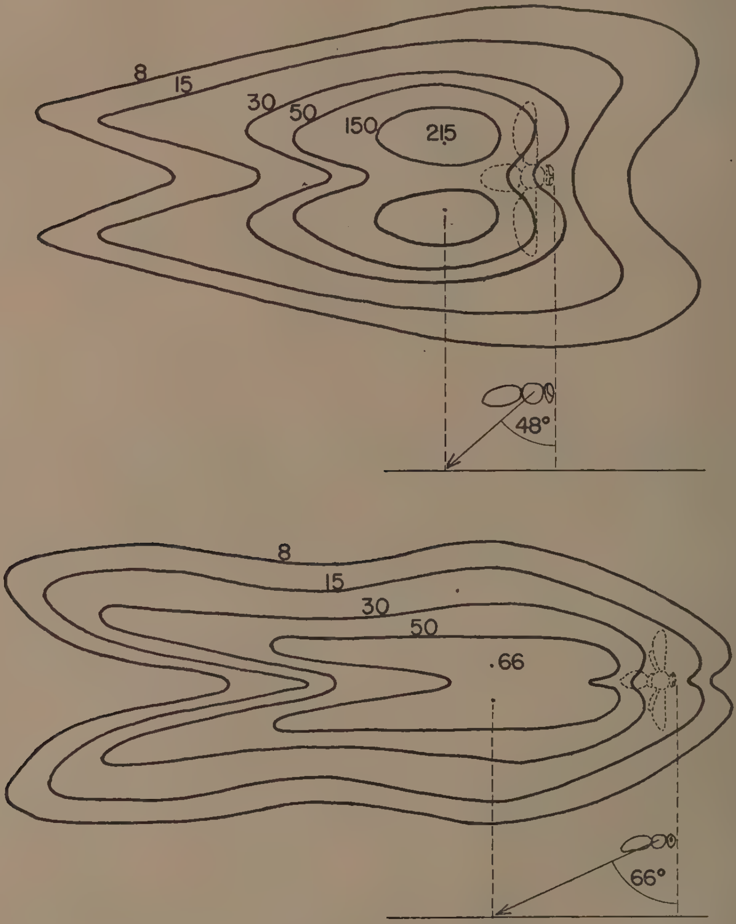


Fig. 5.—The distribution of air speeds in the slipstreams produced by *T. affinis* (above) and the honey bee. Speeds in cm./sec. $\frac{2}{3}$ actual size.

or even three specimens before the area could be completely covered once; about twenty specimens were used. For each species the readings at each point of the grid were averaged, and lines were drawn connecting points of equal air speed (fig. 5). The values of m were obtained by summing these average readings in cm./sec., multiplying by 0·403 to convert from the $\frac{1}{4}$-in. grid squares to square centimetres, by the cosine of the angle of inclination of the slipstream to the vertical to correct for the inclination of the plane of measurement, and by the density of air. The values of the wing action constant, calculated from $m = 4k\rho . Al\theta n$, are 1·94 for *T. affinis* and 1·90 for the honey bee. The striking differences between the slipstream patterns for these two species can scarcely be attributed to the different number of wings, since the bees' wings were not separated at any time during this study. Possibly the bee uses different angles of attack on the up and down strokes, and the anterior bulge on the pattern represents the effect of the more vertical down-stroke, and the posterior bulge the more inclined up-stroke. Part of the difference is due to the different inclinations of the two slipstreams to the plane of observation. A final explanation must await observations on other species; for smaller species special equipment will have to be developed.

The mass mean speed of the slipstream was calculated approximately and multiplied by the mass of air passed through the wings; the resulting figure, the rate of change of momentum, represents the thrust generated. For both species this was somewhat greater than the weight of the insect, but its vertical component was insufficient to support the insect in the air. This apparent anomaly agrees with Hollick's (1940) finding for *Muscina stabulans* by direct measurement of the resultant force, and is explained in Part III, section 3.

Calculated values of m for all species are given in Table IX. The value of m changes with the speed of flight, these values are averages and yield the power to remain airborne at an average speed of flight. Hovering would require rather more power, because less air would be passed through the wings; at high speeds the power to remain airborne would be rather less. This variation is partly due to changes in amplitude and frequency. These changes do not seem to be great enough, however, to account for the changes in speed recorded in section 4. The only other factor which could influence this is the angle of attack which would affect also the value of k. Chadwick and Williams (1949) have already postulated changes in the mean angle of attack. The accurate determination of the power required at all speeds would need a knowledge of the variation in frequency, amplitude, and angle of attack with speed, and is not necessary to this study.

The last column in Table IX gives the power required for support, obtained by substituting the values of m and the basic weights (Table I) in the expression $\frac{M^2g^2}{2m}$. Dividing these figures by the basic weights gives the power required for support per mg. of basic weight; this ranges from 11 erg/sec. for *S. vittatum* to 38 erg/sec. for the bee, and shows, as expected, an increase with increasing weight.

2. The Power Required for Forward Movement.

(a) *Review.*—The work done in overcoming the resistance of the air is the product of the distance travelled and the parasite drag, the latter varying as the square of the speed. The power required thus varies as the cube of the speed. The drag is not very difficult to measure, but data have been published for one insect species only (*Aëdes aegypti*, Walton, 1947). It may be calculated approximately from the dimensions of the insect and aerodynamic formulae (Langmuir, 1938). Its value at a particular speed depends on the dimensions and the attitude of the insect. There are few observations on the attitudes of insects in flight. Poujade (1884) figured *Culex annulatus* and 12 other species representing the more important orders; Magnan (1934) gave rough sketches of the attitudes of some of the species he studied. Wedmore (1932) mentioned that the bee carries its hind legs further forward when flying with a full load. Walton (1947) photographed *Aëdes aegypti* and *Anopheles m. atroparvus* in flight. Séguy (1950) has redrawn many of Poujade's figures, but has added a figure for *Oestrus* in an attitude similar to that found for *T. affinis* in this study.

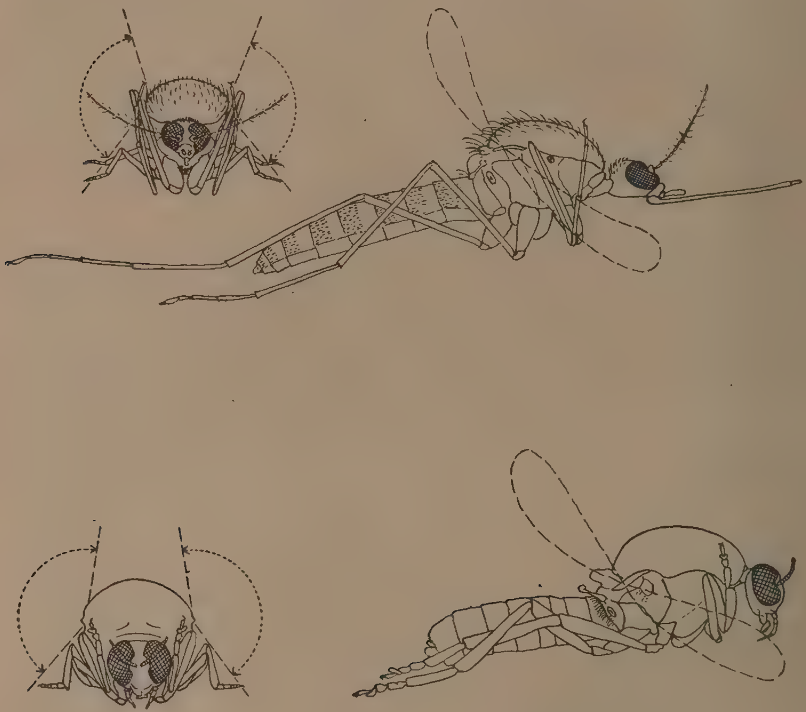


FIG. 6.—The attitudes of *Aëdes nearcticus* (above) and *Similium venustum* in full flight.

(b) *The relationship of drag to speed: experimental.*—Although the positions of the appendages were found to have only a small effect on the drag, care was taken to arrange them in the positions found in the insects in full flight. These positions were recorded photographically for *T. affinis* and by observation for *A. nearcticus* and *S. venustum*, and are shown in fig. 6 and Plate VI. No differences were found between these and other species in their respective families, except that *C. nigripes* extended its front legs forwards unless it was flying strongly. To obtain these positions consistently it was necessary to stimulate the insect with a moving background and a current of air, as in natural flight. The flight attitude of *Drosophila* resembles that of *T. affinis* except that the front tarsi are directed backwards instead of forwards. The smaller species were observed at a magnification of 10 diameters.

The most interesting features of these flight attitudes are the very close folding of the front legs, except perhaps in the tabanids, and the curious interlocking of the last two pairs of legs in the black flies. In this latter group the folding of the front legs is carried out by stages, and they may fly around without completing the femoro-tibio-tarsal flexions, so that the tarsi project above the mesonotum like a pair of masts. This is shown as the normal flight attitude of a bibionid by Poujade (1884). Apart from this, the attitudes are quite different from those figured by Poujade and those photographed by Walton (1947), which are more like the grappling attitude (Plate VI), perhaps as a result of the confinement of the insects. Possibly they should be regarded as flitter attitudes rather than flight attitudes.

The first measurements on drag were made in a simple straight-through wind tunnel. The tunnel consisted of two 4-ft. lengths of aluminium sheet rolled into 6-in. diameter tubes, separated by a lucite working section 9 in. long which was readily removed for manipulating specimens. The air was moved by the suction end of a 6-in. centrifugal blower, driven by a $\frac{1}{4}$ h.p. motor controlled by a variable transformer. Freshly killed specimens, or specimens preserved in alcohol-glycerine, with wings spread and legs and body set in the normal flight attitudes, were mounted on the tip of a horizontal needle projecting through a slit into the working section. The needle was suspended from a torsion head on a phosphor-bronze wire so that the insect faced up-wind in the centre of the tunnel. The other end of the needle carried an aluminium foil vane which was surrounded by a lucite box to provide air damping. Turbulence was controlled by sections of Dufaylite impregnated paper honeycomb of 5 mm. mesh. Air speed was measured with a Pitot tube connected to an oil manometer with a vernier mm. scale, inclined at a slope of 1 in 10. Readings obtained with this were checked with a hot thermopile anemometer. A series of tests were run to measure the drag on the needle with no insect attached; these values were subtracted from the readings obtained with insects. All tests were run on increasing and decreasing wind speeds, to eliminate hysteresis effects.

This arrangement was later modified to the return flow tunnel shown in fig. 7 to minimize the disturbances due to pressure waves from doors closing, people coughing, and other causes. Also, since the drag on the wings in any set attitude has little meaning in evaluating the drag on the vibrating wings, the wings were removed. The drag due to the wings is thus a part of the losses accounted for in the efficiency factor (Part IV).

It soon became clear that the variation in the values obtained for a species was greater than that expected from the variation in its dimensions. It was suspected that this was due to a variable amount of induced drag resulting from the inclination of the body axis to the air flow. To settle this point, the complete aerodynamic balance shown in Plate IV was constructed. This was essentially the same as the original instrument except that the needle carrying the insect was pivoted on a horizontal axis parallel to the axis of the tunnel, on a cradle which was suspended from the same torsion wire. The needle was balanced about this axis by a small chain, and a more flexible oil-damping system was used. A small mirror made it possible for both vertical and horizontal zeros to be seen from the same position. The lower end of the torsion wire was sealed with a hard laboratory cement into a small hole drilled

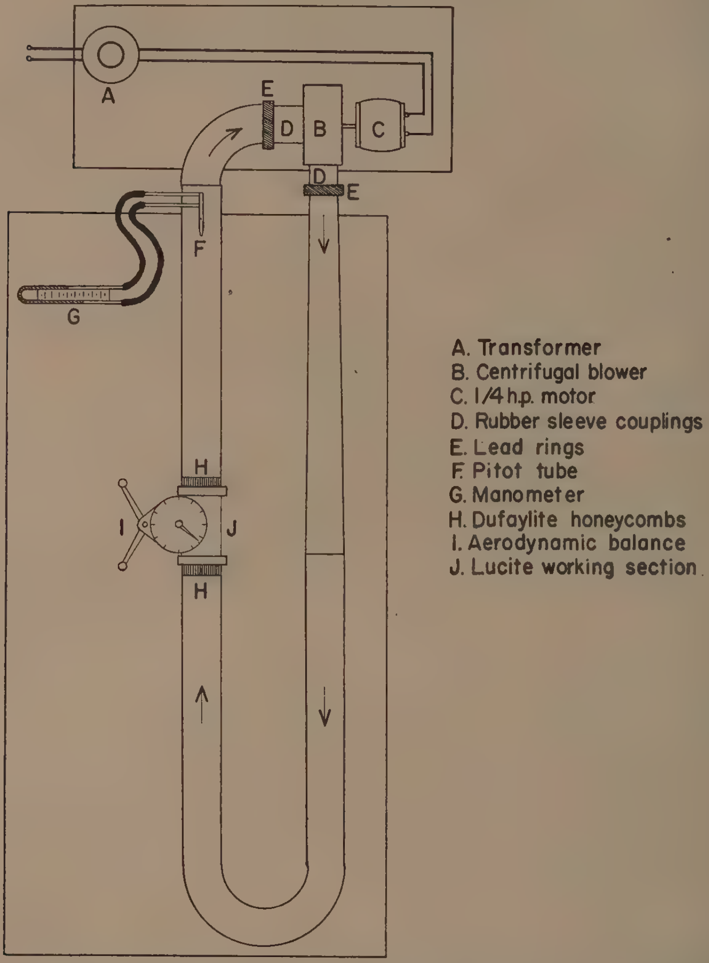

A
E
D
B
C
D
E
F
G
H
I
J
H
A. Transformer
B. Centrifugal blower
C. 1/4 h.p. motor
D. Rubber sleeve couplings
E. Lead rings
F. Pitot tube
G. Manometer
H. Dufaylite honeycombs
I. Aerodynamic balance
J. Lucite working section

Fig. 7.—The arrangement of the wind tunnel used to measure the drag on the body of an insect.

in the top of the cradle, the upper end was held in a chuck in the torsion head. The sensitivity and range of the instrument could thus easily be changed to suit insects of different sizes by changing the wire. Two ranges were used; a force of one dyne at the tip of the needle was balanced by a one degree turn of the torsion head in the high range, and by a two-degree turn in the low range. One fifth of a degree could be measured, or 0·1 dyne in the low range. The chain balance, measuring lift forces, was graduated in dynes and could be read to 0·5 dyne. Parallax was eliminated by using a flattened needle on the torsion head, and a zero index on either side of the pointer for the chain balance. Small corrections had to be subtracted from the drag readings when the lift was high, to compensate for the torsion effect of the chain.

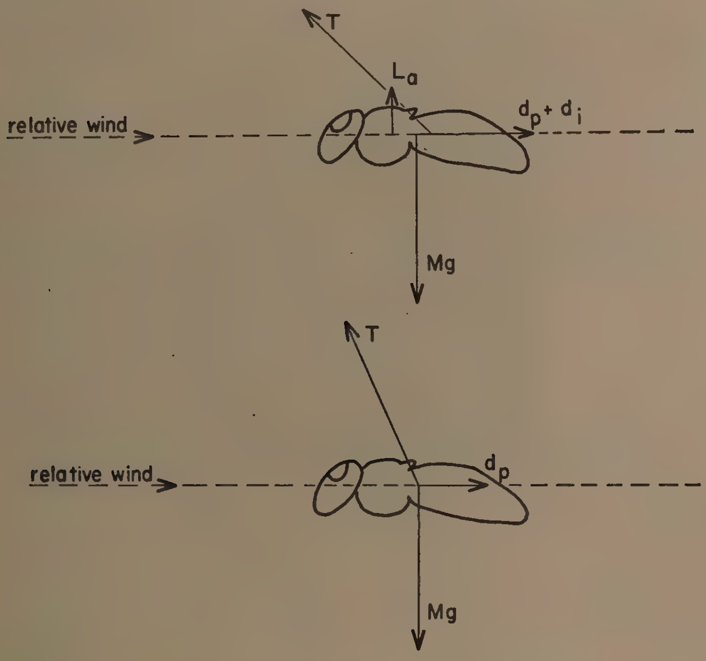
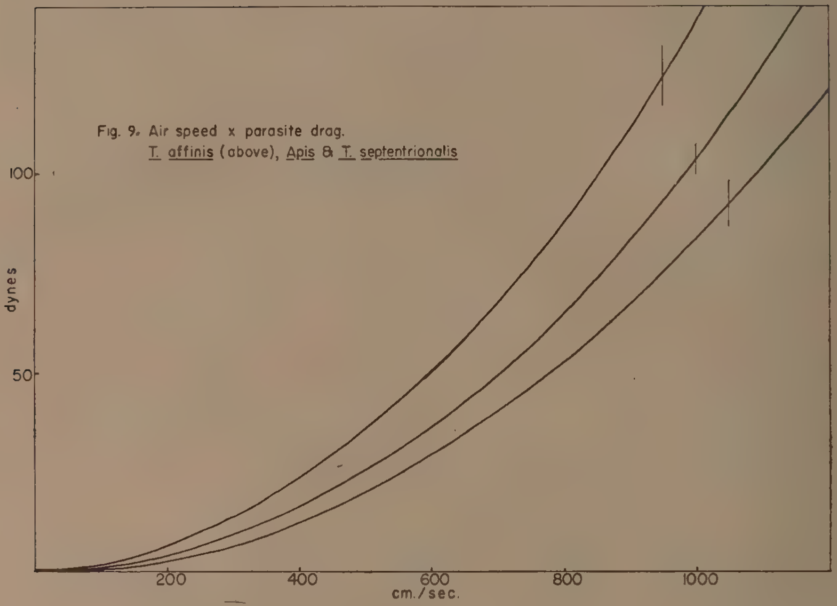
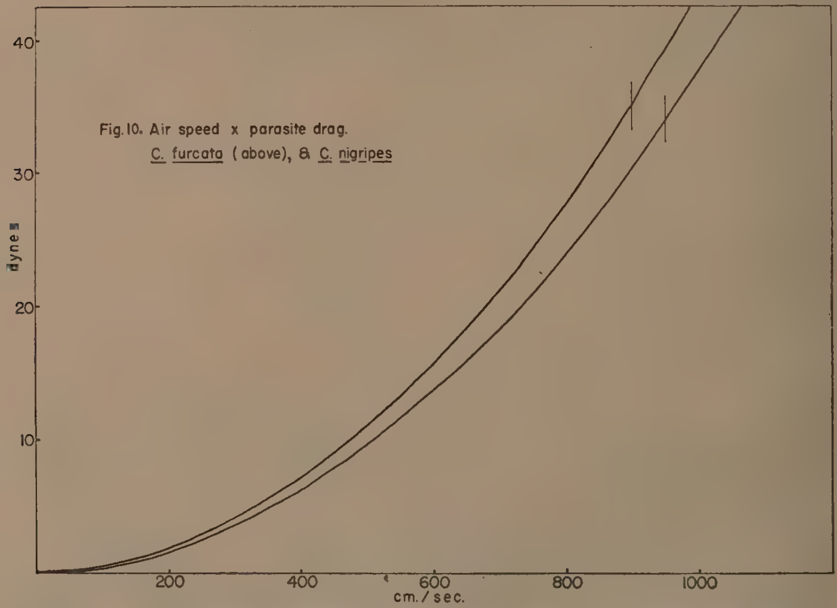


FIG. 8.—The forces acting on an insect in flight. Above, the probable actual disposition; below, the assumed disposition for purposes of calculations.

Using this instrument, it was found that specimens with the wings removed and in normal flight attitudes experienced lifting forces up to about one-third of their weight at maximum speeds of flight. The honey bee gave the highest lift values in proportion to its weight. It is difficult to see just what body surfaces are responsible for providing this airfoil action, but these results were obtained repeatedly with all the insects studied. Readings were then taken with the axis of the insect inclined at different angles to the air flow, when it was found that both lift and drag increased, as expected, with increasing angle. By decreasing the angle a position could be found for which the lift became





Figs. 9–12.—The relationship between drag and air speed. (9) *T. affinis*, *Apis*, and *T. septentrionalis*. (10) *C. furcata* and *C. nigripes*. (11) *A. campestris*, *A. punctor*, *A. nearcticus* and *A. communis*. (12) *S. venustum*, *S. vittatum* and *Drosophila*.

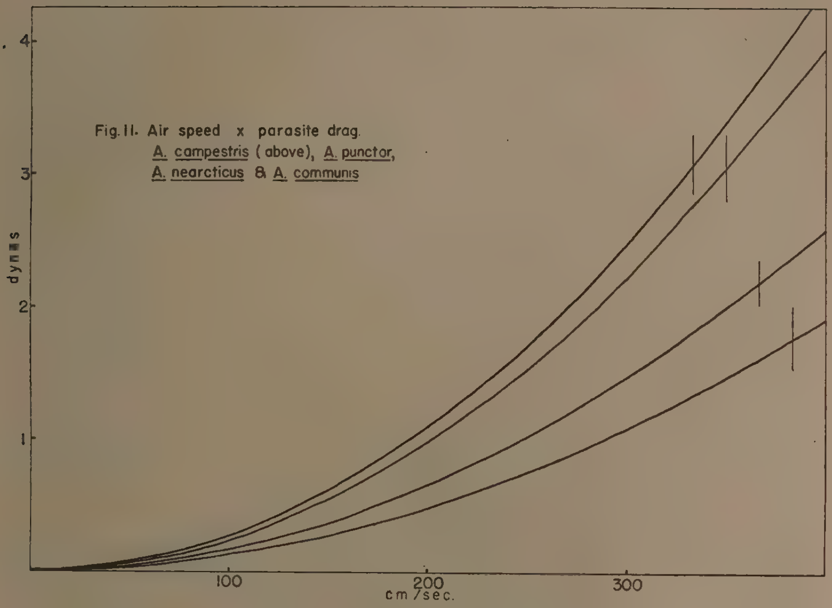


Fig. 11. Air speed x parasite drag.
A. campestris (above), A. punctor,
A. nearcticus & A. communis

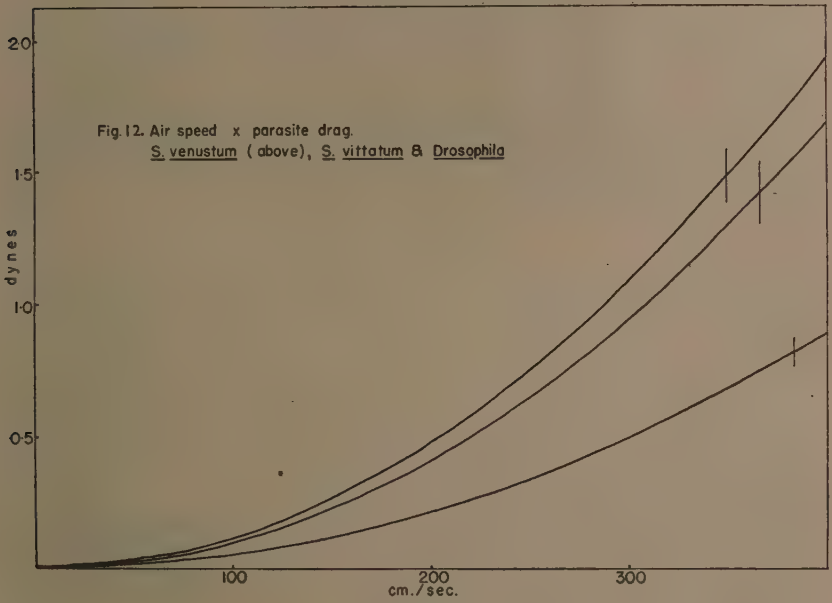


Fig. 12. Air speed x parasite drag.
S. venustum (above), S. vittatum & Drosophila

zero, and the drag a minimum ; for all insects this was definitely " head down " as compared with the normal flight attitude.

No precise definition of the axis of an insect is feasible, so that exact angles of inclination, which profoundly influence the lift, cannot be given. For this reason, and also because it permits a simplification in other phases of the work, the minimum drag was measured, and this was regarded as wholly parasite drag. In other words it was assumed that the work that is actually done against the induced drag is the same as the extra work which would be done directly by the wings if no lift were obtained from the body—as in hovering flight. The power required to support the insect in the air, as already calculated, may then be applied. The assumed and the probable actual dispositions of the forces acting on the flying insect are shown in fig. 8. The airfoil lift is represented as acting in front of the centre of gravity, as required to balance the force system described by Hollick (1940) ; it is shown later that this may be incorrect.

Proceeding on this assumption the curves connecting parasite drag with air speed for all species are given in figs. 9 to 12. Variations in line voltage and motor speed prevented the repetition of readings at chosen air speeds, so that standard errors could not be calculated, but the limits of variation are indicated by the vertical lines across the curves.

The measurement of the drag on the mill arms used for efficiency measurements in Part IV gave an opportunity to check these figures by a rotating arm method. The description of these measurements is given in Part IV, section 2, (*a*). After the drag on the arm itself had been measured, readings were repeated with insects attached in " no lift " attitudes. The drag on the insect was found by subtraction. This was done for *T. affinis* and the bee, and all readings fell within the limits found in the wind tunnel measurements.

The most significant dimensions of these insects in relation to parasite drag are the transverse dimensions of the thorax. The sectional area of the thorax (S) was measured for each species ; the drag × air speed curves were then found to represent equations of the form :

$$d_p = \tfrac{1}{2}\rho C_D S V^2, \quad . \quad . \quad . \quad . \quad . \quad (4)$$

where C_D, the dragco efficient, has values ranging from 1·1 for the larger species to 2·3 for the smaller. The higher values for the smaller species are an expression of the greater proportions of their appendages relative to their bodies.

The swelling of the abdomen of an insect with a large meal has little influence on the drag. Much of the volume of the meal is taken up by a reduction in the size of the large air sacs immediately anterior to the crop (Evans, 1935). Changes in external configuration take the form of an increase in length, and an increase in girth beginning at the anterior end of the abdomen. The sectional area of the abdomen only comes to exceed that of the thorax in exceptionally fully fed specimens. As the crop weight increases, the centre of gravity moves backwards, and the inclination of the body to the relative wind increases. This automatically compensates for the greater weight by giving the slipstream a smaller inclination to the vertical and by increasing the lift due to body surfaces.

3. THE TOTAL POWER OUTPUT REQUIRED : DISCUSSION.

The total power output required is the sum of that needed to maintain the insect in the air, and that needed for forward movement, and may be written:

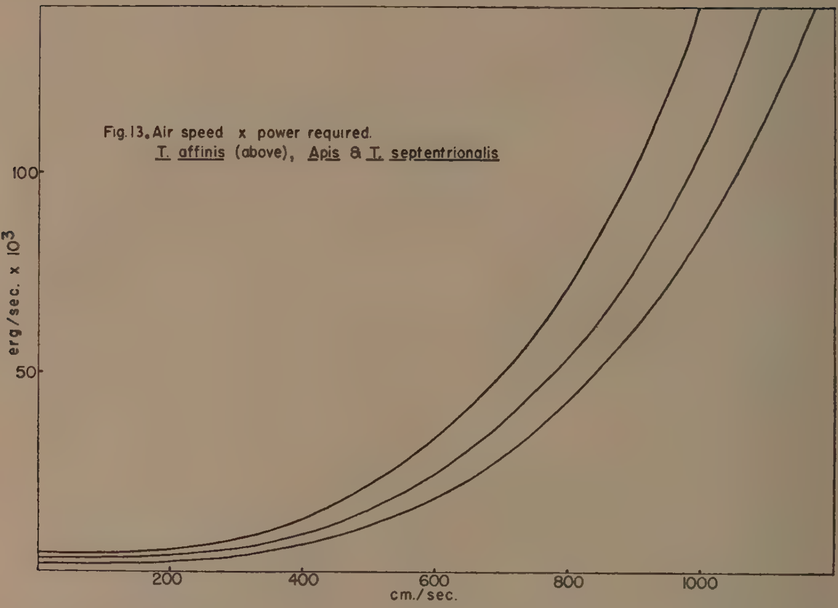
$$\text{Power} = \frac{M^2g^2}{8k\rho . Al\theta n} + \tfrac{1}{2}\rho C_D S V^3, \qquad . \quad . \quad . \quad (5)$$

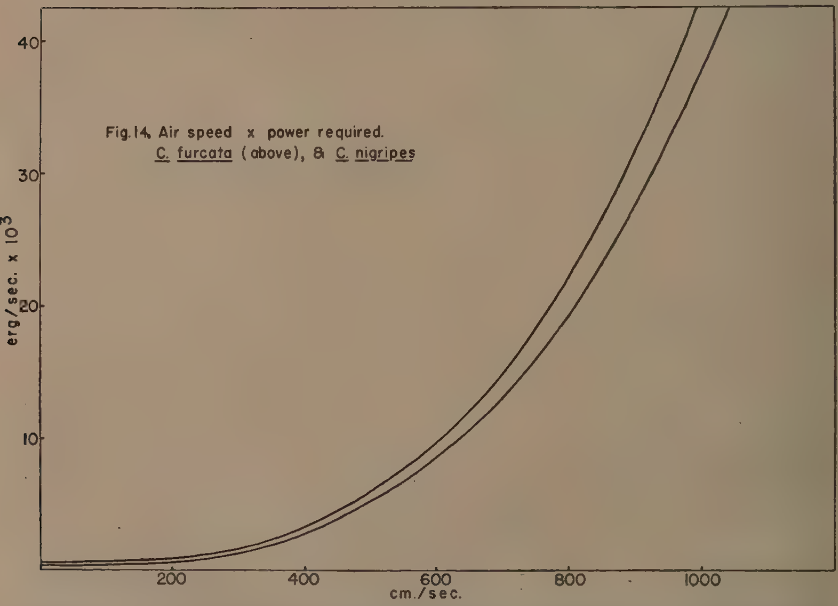
where C_D ranges from 1·12 for insects of moderate size to 2·3 for small insects, and $k = 1{\cdot}95$ for Diptera and 1·90 for the bee. Curves connecting speed and total power output required, obtained by substituting the experimental values for each species from Part III, sections 1 and 2, in equation 5, are shown in figs. 13 to 16. In fig. 15 the curve for *A. nearcticus* starts below that for *A. communis*, but crosses this at about 100 cm./sec.; the curves for *A. campestris* and *A. punctor* are too close to be shown separately below 100 cm./sec.

The second term in the expression for power (5) varies as the square of the linear dimensions, while the power available should vary as $W^{0.73}$ or as $L^{2.19}$ (Hill, 1950; Ellenby, 1951), so that the maximum speed of flight should increase with increasing size. On the other hand, the numerator of the first term varies as $\underline{L}^6$, and the denominator approximately as $\underline{L}^{2.8}$ (the variation of frequency with size is somewhat indefinite). The power for support then varies as $\underline{L}^{3.2}$. Thus, with increasing size the power required to maintain an insect in the air must eventually become greater than that which the muscles can develop. This, as much as the difficulty of diffusion respiration (Krogh, 1941), may set a limit to the size of flying insects. Furthermore, since the load which may be carried depends, providing there is room for it in the body, on the power available over and above that required to lift the basic weight of the insect, in insects of similar characteristics it should vary as $a\underline{L}^{2.19}–\underline{L}^{3.2}$. The load per unit weight should vary as $a\underline{L}^{-0.81}–\underline{L}^{0.2}$. In fig. 17 a curve of this function is drawn on the same axes as a scatter diagram of the basic weight and maximum load data from Tables I and III. A relationship of this type agrees quite well with the data for the two species of *Tabanus*, the two species of *Chrysops*, and three of the *Aëdes* species. The aberrant mosquito is *A. communis*.

Hollick's flies (1940, p. 365) must have gone into nose-dives when released from their mounts, not only as he supposed because the resultant passed behind the centre of gravity, but also because without forward movement to contribute the lift from the body surfaces, the vertical component of the resultant force from wing action was insufficient to support them. The mean value of this vertical component calculated from Hollick's figures was 24·2 mg., the mean weight was 31 mg. Incidentally, the horizontal component of the resultant force was 20·6 mg., equivalent to the parasite drag on *Chrysops furcata*, a fly of similar size, at a speed of nearly 700 cm./sec., which is far in excess of the speeds Hollick observed. Part of this horizontal component must surely be regarded as balancing an induced drag, and thus indirectly supplying the deficiency in lift.

It is noteworthy that the bee, which gave the greatest lift readings in the wind tunnel in proportion to its weight, also gave the slipstream with the greater inclination to the vertical, i.e., the thrust with the smaller vertical component (fig. 5).





Figs. 13–16.—The relationship between air speed and power required. (13) *T. affinis*, *Apis* and *T. septentrionalis*. (14) *C. furcata* and *C. nigripes*. (15) *A. campestris*, *A. punctor*, *A. nearcticus* and *A. communis*. (16) *S. venustum*, *S. vittatum* and *Drosophila*.

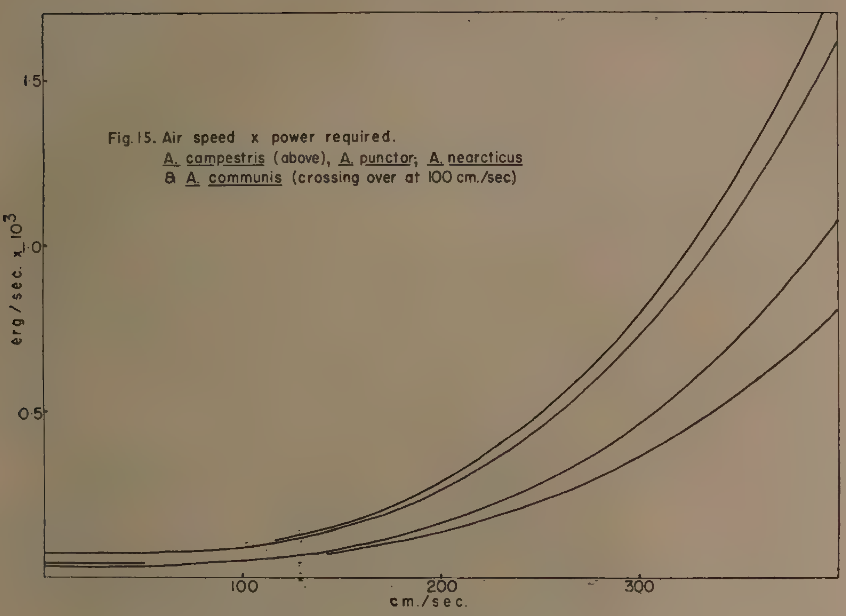


Fig. 15. Air speed x power required.
A. campestris (above), A. punctor; A. nearcticus & A. communis (crossing over at 100 cm./sec)

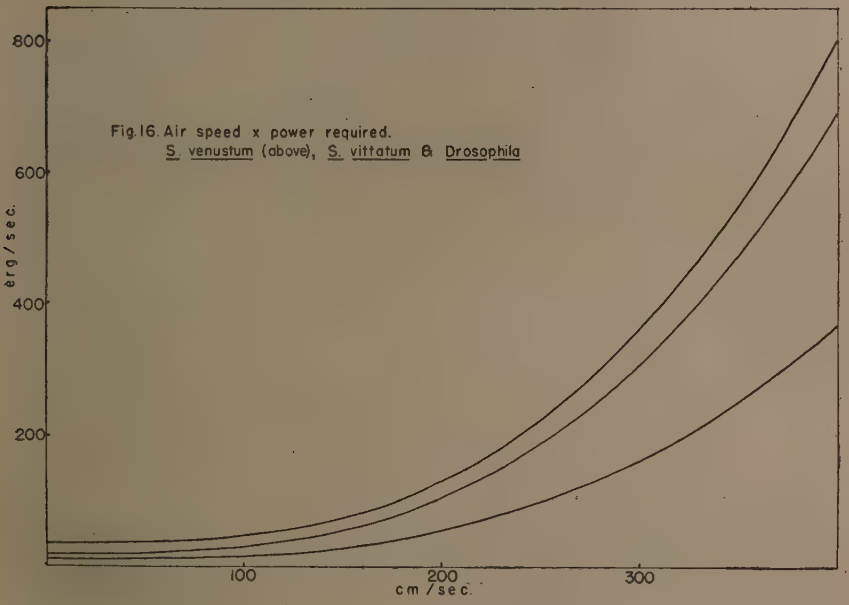


Fig. 16. Air speed x power required.
S. venustum (above), S. vittatum & Drosophila

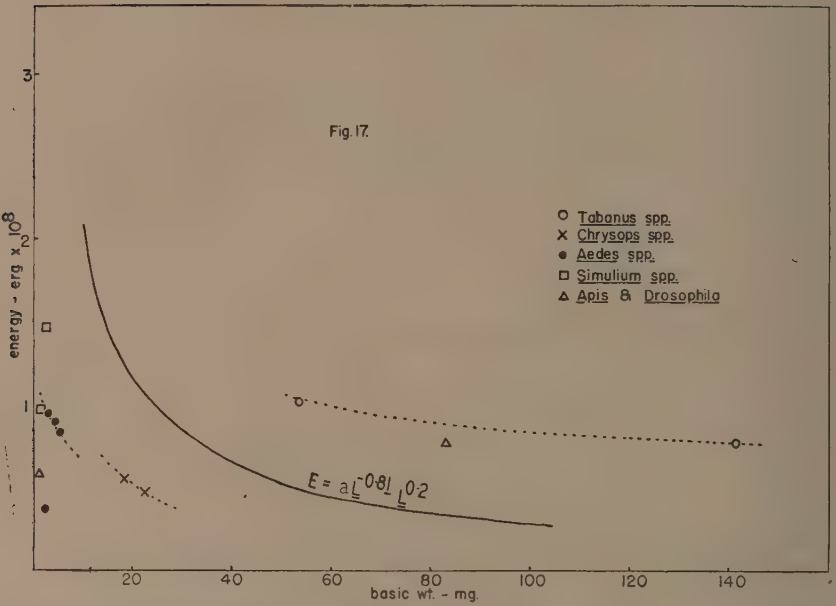


FIG. 17.—The relationship between the basic weight of an insect and the energy carried per unit weight.

The centre of gravity of an insect moves backwards with increased feeding and fat body or ovary development, and cannot be regarded as fixed in position. When the resultant force from wing action passes behind the centre of gravity, the tendency to go into a dive will be offset if the centre of pressure of the relative wind, the point at which the drag acts, is above the centre of gravity. The airfoil lift (fig. 8) may then act behind the centre of gravity, as it would if contributed by the ventral surface of the abdomen. On the other hand, if, as seems possible, the drag force acts below the centre of gravity, the tendency to dive will be aggravated. Perhaps the attitude observed in black flies with the front legs stretched upwards represents an attempt to correct this when flying at low speeds on an empty stomach.

PART IV.—EFFICIENCY.

1. GENERAL CONSIDERATIONS.

Energy losses occur both inside and outside the flying insect. Those within the body result in the work which the flight muscles can do being proportionately less than the chemical energy of the materials fed to the insect; this proportion is the metabolic efficiency. It may be subdivided into nutritional and muscular efficiencies. The energy losses here take the form of incomplete absorption; the work expended in overcoming the resistance of body colloids

(Brody, 1945); and resting metabolism, the energy required to maintain life processes other than flight.

The losses outside the body necessitate more work being put into the movement of the wings than that theoretically needed to support and propel the insect through the air. The ratio of the work theoretically needed to that put into the wings is a combination of the mechanical and the aerodynamic efficiencies. The latter term should not be confused with the empirical aerodynamic efficiency used in aeronautics and expressed in ton miles per B.H.P. hour. The losses are due to inertia and to friction between the axillary sclerites and the notal processes and between the radial veins and the pleural processes and to wasted kinetic energy in the slipstream.

The combined effect of these energy losses is that the chemical energy consumed by the flying insect is much greater than the energy theoretically needed (Part III), and the proportion between the two is here referred to as the overall efficiency. This term is preferable to the gross efficiency of Brody (1945), as his definition can hardly be applied to an insect in flight.

There is no published work on the metabolic efficiency of insects. The principal difference between insect muscle and that of vertebrates is the replacement of creatine phosphoric acid by arginine phosphoric acid (Baldwin and Needham, 1933; Heller, 1936; Gilmour, 1948). Hexose phosphates and adenosine triphosphate are present in similar quantities (Albaum and Kletzkin, 1948; Calaby, 1951), Rockstein (1950) stated that the chemical processes of glycogen metabolism in insects follow a pattern similar to that in higher animals. It seems reasonable, then, to expect that similar efficiencies are shown by the two types of muscle. Hill (1950) described the way in which this efficiency varies with speed and load, and in common with most other authors he placed the maximum value at about 0·25. Gemmill (1942) gave from 0·17 to 0·27; Zeuthen (1942) assumed an efficiency of 0·25 in calculating the limiting speed of flight of the pigeon. However, efficiency decreases with increased speed of operation and, even allowing for their small size, the flight muscles of insects function at a very high speed. Sotavalta (1952) has calculated the efficiency of insect flight muscles using data from various sources. His values range from 0·015 for *Drosophila* to 0·2 for *Apis*.

The resemblance between the wings and an aircraft propeller has already been mentioned. Von Holst (1943, 1948) stated that the insect wing resembles a propeller in all essential features, and that it may have an efficiency up to 0·7. The efficiency of an aircraft propeller depends on the speed, actually on the propeller modulus, the ratio of the forward speed to the tip speed, and reaches a maximum of about 0·85 when this is about 0·36 (Durand, 1934; Bairstow, 1939). Vanderplank (1950) suggested that the ratio of wing tip speed to air speed in insects is constant at about 2·3, i.e., a " propeller modulus " of 0·43, equivalent to an efficiency of 95 per cent. of the theoretical maximum or about 0·66. Williams and Galambos (1950) showed that the flying insect produces a polarized flow of air from front to rear during about 85 per cent. of the wing beat cycle, which may perhaps be regarded as suggesting an aerodynamic efficiency of this order.

The highest overall efficiency which could possibly be expected then is the product of these two efficiencies, 0·25 × 0·66, or about 0·165, but it is unlikely that maximum muscular and aerodynamic efficiencies would be achieved under the same conditions. The independent measurement of these two efficiencies experimentally would be difficult, and is unnecessary for present purposes.

No direct measurements of the overall efficiency of insects in flight have been made. From the unpublished data of Williams (Chadwick, 1951) on power output, and Chadwick's figures for metabolism in flight, a value of 0·0264 may be calculated for *Drosophila.* Chadwick (1953) has arrived at a value of 0·04 for *Vanessa* from power output data by Magnan and Planiol (1933) and measurements of metabolism by Krogh and Zeuthen (1941). A method of measuring the overall efficiency directly was developed as follows.

2. The Measurement of Efficiency.

(a) *The equipment and procedure.*—Initial investigations were made of the duration of flight on measured amounts of food, by attaching cotton threads to the mesonotum of *T. affinis* with wax. The insect was then allowed to fly freely until exhausted. Every time it stopped flying it was rested on a small platform for one minute ; it was considered exhausted when three successive flights were all of less than 15 seconds' duration. When exhausted, the fly was fed a measured amount of sugar solution. It was then flown again in the same manner, and the duration of flight to exhaustion was recorded. The end-points, especially on glucose solutions, were quite sharp. The figures obtained in this way are given in Appendix C. (*T. affinis* 1/1 to 2/1). This did not allow the measurement of distance flown, and the habit of flying in a loop and alighting on the thread was troublesome.

It was then observed that when an insect was harnessed to the tip of a light arm which was free to rotate about its other end, although potentially supported by the arm, the insect would in fact support its own weight when it was flying. That is, if the arm is balanced before attachment of the insect, it remains so with an insect attached and in flight, without any counterbalancing of the insect. In other words, the considerations in Part III regarding the power required by the insect in free flight apply equally well to the insect in flight tethered on such an arm or flight mill. The time and the distance flown by an insect on a flight mill can be determined. If the frictional and aerodynamic drag of the mill is known, the speed and distance can be corrected for the additional work which is done against this force. The work done by an insect in flight may be expressed as a fraction of the energy contained in the food fed to it ; this fraction is the overall efficiency.

This same procedure of flying on a mill yields direct information on flight range and flight speed, after the corrections for the drag of the mill have been applied.

Two trial mills of this type were constructed in the field in 1951. The dried stems of a local grass were cut to a suitable length and slits made in them near one end ; $\frac{3}{4}$-in lengths of glass tubing, 3 mm. outside diameter, were sealed at one end and the other ends were cemented into these slits. The arms were balanced by inserting suitable lengths of wire into the lumens of the short ends of the straws after normal aluminium foil insect mountings (Part III) had been attached at the tips of the long ends. The arms were then pivoted on steel needles. The data on *T. affinis* (2/2 to 7/3), *T. septentrionalis* (1/0 to 3/1) and *Aëdes flavescens* (1/0 to 1/2) in Appendix C were obtained on these simple mills. *T. affinis* specimens were flown on the longer mill which gave a circumference of 1·79 metres, the mosquito on the small mill with a circumference of 1·08 metres; both mills were used for *T. septentrionalis*.

The combined aerodynamic and frictional drag on the mill arms at various speeds was measured by winding fine silk threads on the glass tubes, and passing these over very light, low friction pulleys. Pans, just not heavy enough to keep the mill in motion, were attached at the lower ends, and various weights were added to these; the limiting speed of the mill was measured for each weight. The equivalent drag at the tip of the arm necessary to balance the couple exerted by these weights was then calculated, and plotted against the limiting linear speed of the tip. In correcting the figures for flight speed for this drag, two curves were drawn on the same axes of speed and power, one for the insect in free flight, and one for the insect on the mill (fig. 18). The power required for support was omitted. For a given mill speed the equivalent free speed was then found by reading across from the mill curve to the free flight curve. Proportional corrections were then made to the distances. Krogh and Weis-Fogh (1952) have described a method whereby this rather tedious process is eliminated by compensating for the drag of the equipment during the flight, but it would be difficult to apply it to mills for single insects in the field. With these mills the equivalent drag on the tip of the mill was about twice that on the insect, so that the insects were operating against drag forces about three times the normal value. The possible influence of this on efficiency is considered later. The results obtained with these mills were sufficiently promising to justify the development of the equipment shown in fig. 19 and Plate V, fig. 2, which provided automatic records of the times and distances of flight.

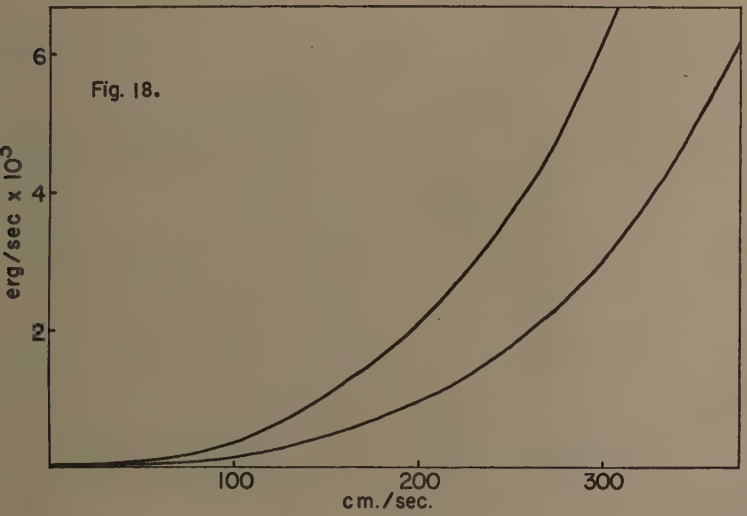
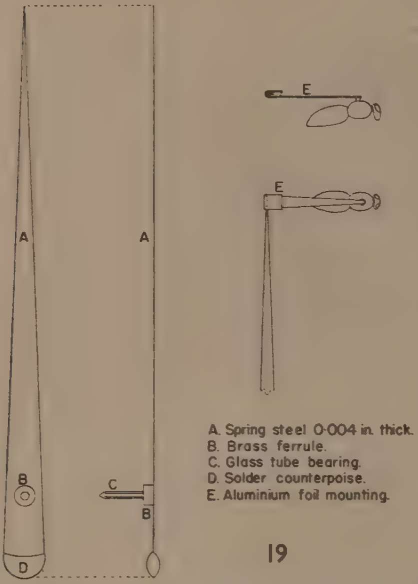


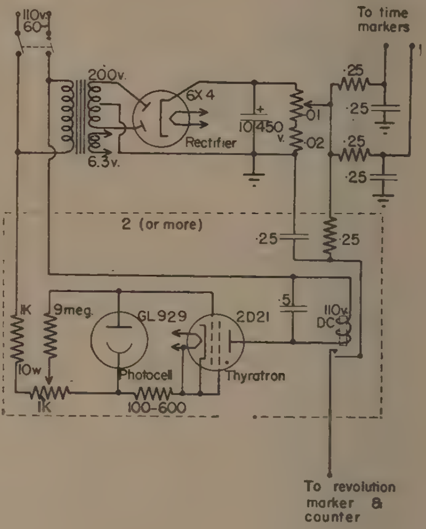
Fig. 18.—Typical curves connecting the power required in free flight (below), and on a flight mill, with the air speed. Used to correct for the drag of the mill. *Apis*.

The desirable features of flight mill arms in order of importance are: low aerodynamic and frictional drag, a convenient and readily adjustable attachment for the insects, durability, low moment of inertia, and a broad area near the centre. This area is needed to interrupt the light falling on a photocell for a long enough period to trip the relay at all likely speeds of rotation. The straws used initially had high drag and changed in shape under changing humidities. They were easily damaged, and damage meant that a new mill had to be calibrated. Among other materials tried were fine aluminium wire and tubing, steel wire, plastic strips, artificial drinking straws and nylon monofilament, but strips of feeler gauge steel were finally preferred. Two sets of mill arms were made from this material, giving circumferences of 0·5, 0·75, 1·0, 1·5 and 2·0 metres. The thickness ranged from 0·002 to 0·01 in. The arms were balanced by adding solder to the short end, edges were tapered off, and all arms were checked to ensure that there was no lift and that the drag was the same for both directions of rotation. The details of a 1·0 m. arm are shown in fig. 19, together with the method of attaching insects. Insects were attached at the tips of the arms with wedge-shaped pieces of aluminium foil, 0·001 in. thick for the smaller species, and 0·005 in. thick for the larger. These were fastened to the insects on the mesonotum with wax as already described. The broad end was folded round the tip of the mill arm, and also sealed with a minimum amount of wax. The holder, Plate V, figs. 1 and 2, was helpful in ensuring that the insect was attached with its body axis perpendicular to the



E
E
A
A
B
C
B
D
A. Spring steel 0·004 in. thick.
B. Brass ferrule.
C. Glass tube bearing.
D. Solder counterpoise.
E. Aluminium foil mounting.

19



110v. 60~
To time markers
200v.
6X4
Rectifier
6.3v.
10|450 v.
·01
·02
·25
·25
·25
·25
2 (or more)
·25
·25
·5
110v. DC
1K
9meg.
GL929
2D21
10w
Photocell
Thyratron
1K
100-600
To revolution marker & counter

20

FIGS. 19, 20.—(19) A flight mill arm showing the method of mounting the insect. (20) The circuit diagram for the photoelectric recording system.

arm, and, as nearly as could be judged, at the normal inclination to the horizontal. Minor adjustments to correct for irregularity in attachment of the insects could be made by twisting or bending the foil. *Drosophila* was lightly anaesthetized with ether before mounting, the other species with carbon dioxide. The mill arms were pivoted on steel needles embedded in the ends of $\frac{1}{4}$ in. aluminium tubes. These were adjustably mounted on $\frac{3}{8}$ in. horizontal brass rods which also carried the photocells and the landing " mushrooms " described below. The equivalent drag at the tip of each of these arms was approximately the same as that on the insect with which they were used, that is, about half that of the straws, except for the 0·5 metre size, which had several times the drag on *Drosophila*. A few insects showed a tendency to rest a part of their weight on the arm ; this was immediately obvious, since the arm would drop until the inside of the glass tube bearing came in contact with the pivot, and further loading would curve the arm downwards. Any insect which did this persistently was rejected.

To obviate the necessity for counting revolutions of the arms, and to permit two insects to be flown at the same time, a photoelectric counting device was used. The circuit diagram for this is given in fig. 20. Briefly, the current change resulting from the interruption of the light falling on a photocell as the arm passed over it was amplified and used to trip a relay. This fed a direct current into an electric counter and to a stylus which recorded a dot on electrosensitive paper moving under it on a kymograph drum. The same system supplied suitable current to record a time trace marking 10-second and 1-minute intervals. A 1-ft. diameter drum, spiralling 1 in. per revolution, was used, giving a total tracing of about 18 ft. This enabled all normal flights to be recorded, two at a time, without changing paper. This equipment (Plate V, fig. 2) thus gave the total distance travelled by the insect, as well as the duration of any rest periods, and the speed and acceleration at any time. A typical flight record sheet is shown in fig. 21.

The landing " mushrooms " (Plate V, fig. 2 and Plate VI) consisted of plastic discs 4 cm. in diameter and with a matt surface, pressed between two hot watch-glasses to curve them. These were mounted on steel wires passed through corks threaded on the brass rods which carried the flight mill arms. Their positions could be adjusted so that when they were swung upwards they came into the flight path of the insect on the arm. When an insect ceased beating its wings, the mushroom was swung up and the insect was allowed to rest on it for a period of one minute. Initially, the insects were offered distilled water while resting, but this was soon found to be unnecessary with the 25 per cent. sugar solution. At the end of the minute rest the mushroom was swung down and the insect resumed flying.

Trial flights were made on 50 per cent. and 10 per cent. glucose solutions. Some flights on the former stopped apparently on account of desiccation, since they were resumed when distilled water was given. On 10 per cent. solutions droplets of clear fluid were sometimes passed ; tested with a refractometer these showed 1 per cent. of sugars. A 25 per cent. solution of glucose was fed on all other flights, except for *Drosophila*. Most insects took this readily from the end of the pipette, although some difficulty was experienced with mosquitoes and with the honey bee. The mosquitoes would often insert the proboscis into the tube and vigorous movements could be seen at the base of the organ, but

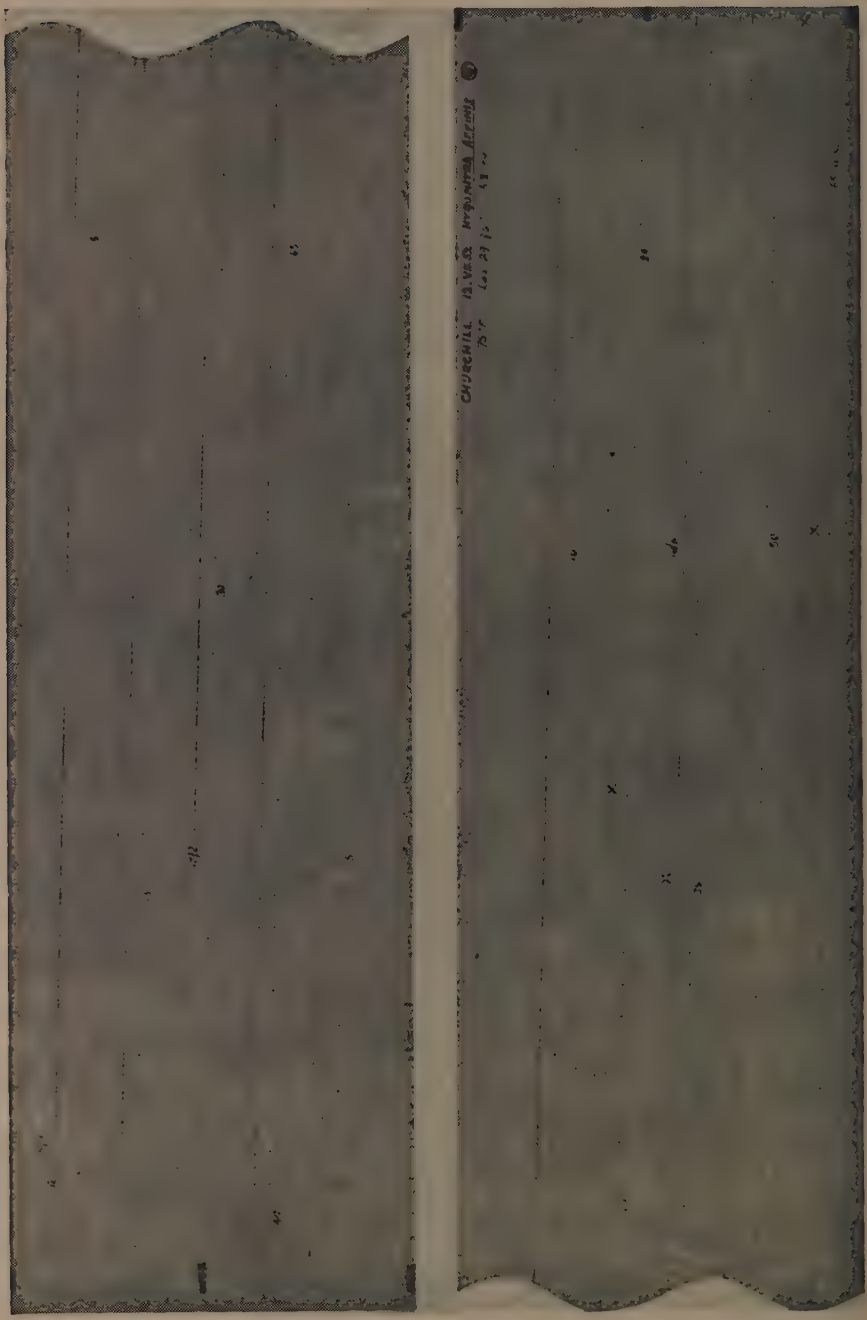


FIG. 21.—A typical flight record sheet.

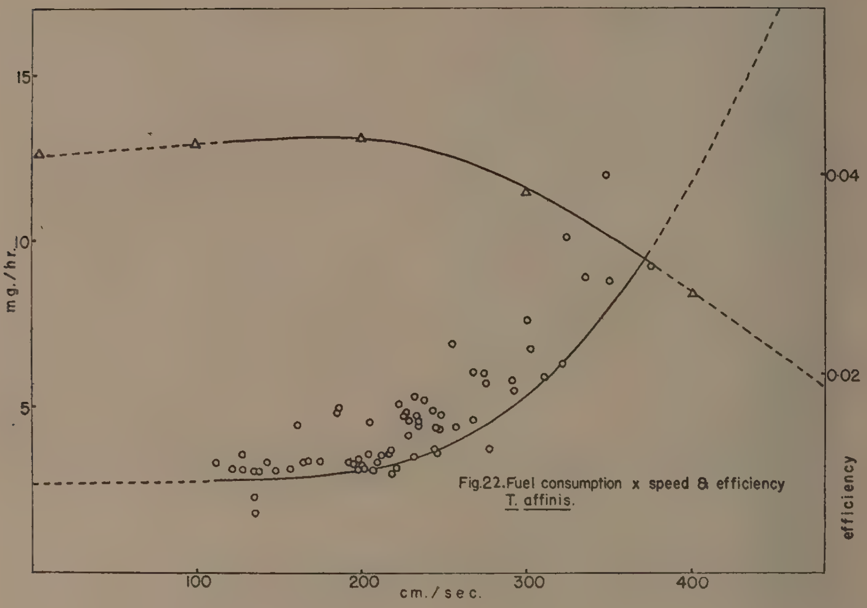
no fluid would be taken. The honey bee fed more readily from exposed droplets on waxed slides. 5 per cent. solutions were used for *Drosophila* because the smallest volume of 25 per cent. solution which could be fed accurately gave inconveniently long flights. This apparently resulted in an accumulation of water in the body; weights were higher after several flights than after first flying out. The basic weight of this species was obtained from specimens after the first flight. *T. affinis* and *T. septentrionalis* (2/1 and 3/1) were also flown on sucrose solutions; continuous flight until nearly exhausted could only be obtained if the insect were rested for 10 to 15 minutes after feeding.

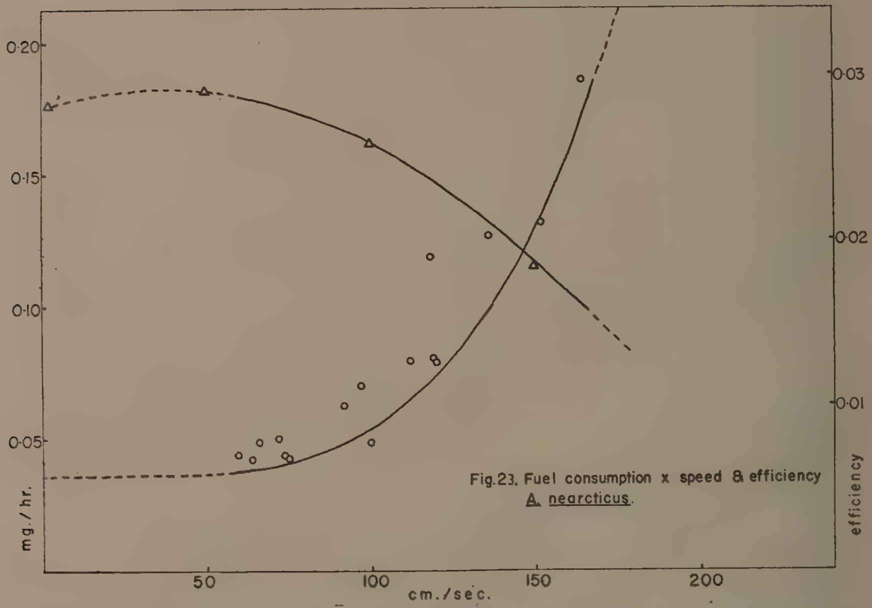
There was a great deal of variation in behaviour between individuals in most species. Some insects would fly and feed very readily, and several sets of figures could be obtained from them; others, after spending 4 or 5 hours flying to exhaustion, would then refuse to feed or fly further. The data obtained from this work with speeds and distances corrected for the drag of the mill arm are given in Appendix C and summarized in Table X. Maximum speeds in a short burst were measured over 100 revolutions of the mill used, that is, in general 200 m. for *T. affinis*, 50 m. for *Drosophila* and 100 m. for the other species, or from 6000 to 15,000 times the body length. The maximum non-stop distance is included as an index of the behaviour of the insect. Atmospheric temperatures and pressures were recorded, but corrections for them were not made; the increase in the power required to overcome drag at higher air density is nearly balanced by the power saving in supporting the insect.

TABLE X.—*Summary of data obtained with flight mills; distances flown and speeds of flight on measured amounts of sugars.*

Species and number of flights.	Total sugars fed (mg.).	Total time of flight (hours).	Total distance flown (km.).	Speed (cm./sec.). Mean (max.).	Consumption (mg./hour). Mean (Max.).
Tabanus affinis (76) .	221·7	53·90	398	206(375)	4·12(11·99)
T. septentrionalis (11) .	12·70	3·14	31	268(283)	4·05(5·61)
Aëdes flavescens Müller (3)	1·1	4·22	22	147(159)	0·261(0·288)
A. nearcticus (16) .	1·98	29·10	94	90(164)	0·0679(0·164)
Simulium venustum (16)	1·93	21·80	120	152(201)	0·0883(0·169)
S. vittatum (3) . .	0·27	2·11	19	247(271)	0·130(0·138)
Apis (16) . . .	41·78	6·17	57	258(352)	6·77(10·5)
Drosophila (22) . .	0·361	14·65	75	142(178)	0·0243(0·348)
Totals (163). .		135·09	816		
Averages (24) .		16·89	102		
Averages per flight		0·83	5		

To determine the influence, if any, of the reduced air speed on the efficiency, a series of tests were made with *T. affinis*, in which the same specimens were flown first on the normal mill, i.e., against twice the drag on the body, then on the same mill to which circular baffles were added to increase the total drag firstly to three times and then to four times that of the insect alone. To guard against possible fatigue or ageing effects, the tests without baffles were then repeated (Appendix C, *T. affinis*, 14 and 15). Efficiencies were calculated for each of these flights separately by the method used below (formula 6); there were no significant differences between the values obtained under the three





Figs. 22–25.—The relationship between air speed, fuel consumption and efficiency. (22) *T. affinis.* (23) *A. nearcticus.* (24) *S. venustum.* (25) *Apis.*

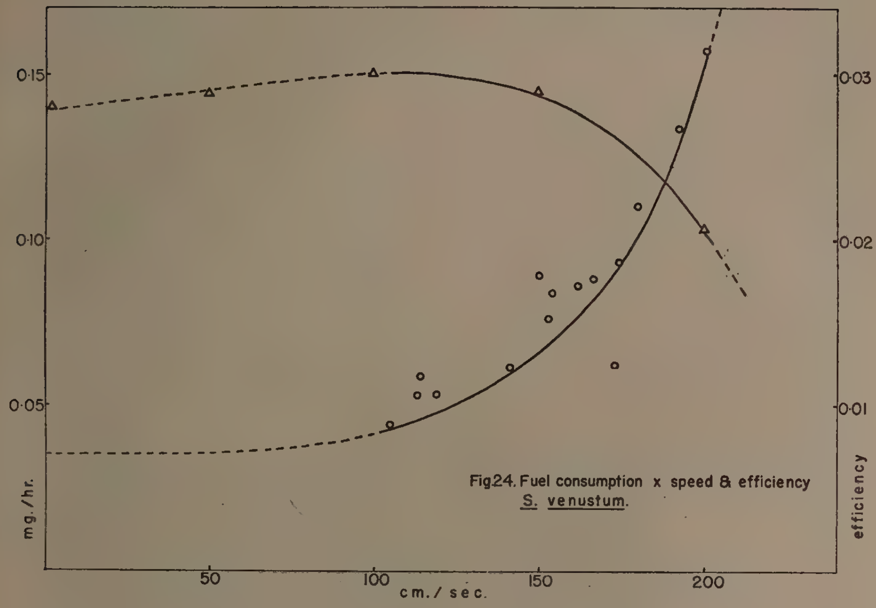


Fig. 24. Fuel consumption x speed & efficiency S. venustum.

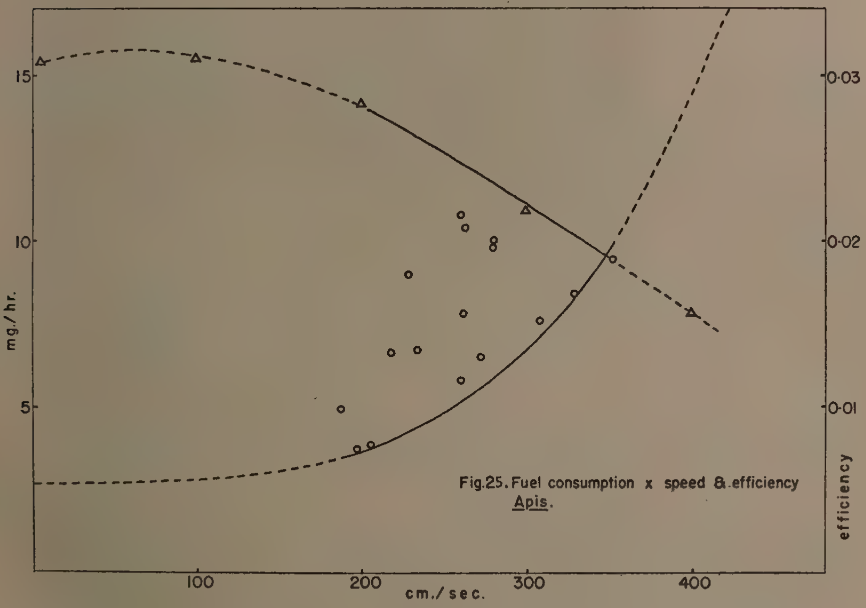


Fig. 25. Fuel consumption x speed & efficiency Apis.

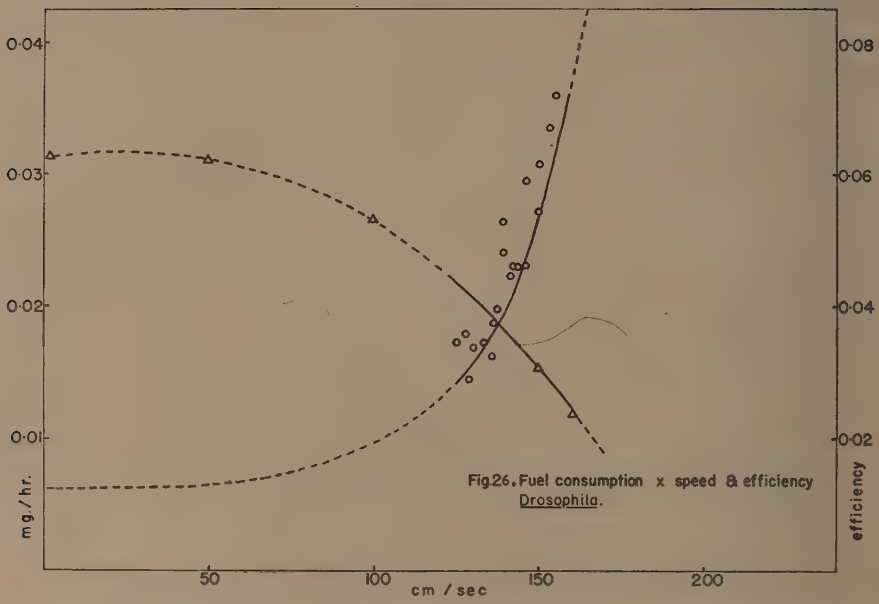


FIG. 26.—The relationship between air speed, fuel consumption and efficiency. *Drosophila.*

conditions ($P = 0{\cdot}05$). If the slowing effect of the mill has any influence on efficiency, this is too small to be detected by this method over this range of speeds. It appears, therefore, that efficiency varies more with the rate at which the muscles are working than with air speed, in other words that most of the energy loss is metabolic rather than aerodynamic.

(b) *The interpretation of the results.*—Probably the most important errors which arise in this method are:

(1) A reduction in flexibility of the mesonotum resulting from the attachment of the arm.

(2) Wasted effort resulting from inaccuracies of mounting.

(3) Wasted effort resulting from attempts of the insects to fly in directions other than those to which they are constrained.

(4) Additional friction at the pivot when insects attempt anything other then level flight.

(5) The effect of drafts.

(6) Additional thrust obtained when the slipstream acts against a solid surface below or behind the insect.

(7) The carry-over of energy reserves from one flight to the next.

All of these except nos. 6 and 7 tend to reduce the performance. Error no. 6 is equivalent to the wall error experienced in wind tunnel work, which is regarded as negligible if the diameter of the tunnel is more than 7 times the dimensions of the test object. Presumably in this work it can be neglected if the flying insect has a clearance from solid surfaces more than 7 times its length. This was always so except for the momentary passage of the fly over the arm carrying the photocell and landing mushroom in a few tests with *T. affinis*. When there was a carry-over of energy this was usually obvious, and the results were discarded. Some aberrant points in the graphs (figs. 22 to 26) may be due to this error.

Using the data in Appendix C, curves were first drawn connecting true air speed with food consumption (figs. 22 to 26). The food consumption was corrected for the difference in weight between the specimen and the mean basic weight of the species by multiplying it by the basic weight over the approximate average weight of the specimen during the flight, viz., its flown-out weight plus half the weight of the meal fed to it. Each curve was drawn as an envelope to the points rather than through them, because of the nature of the errors. The curve for *T. affinis* was drawn first, since the data for this species were the most complete. Where the data for other species left room for doubt regarding the shape of the curve, it was drawn in conformity with that for *T. affinis*. Wigglesworth's (1949) minimum fuel consumption rate was used for the consumption of *Drosophila* at zero speed, since no flights at low speed were made by this species. The average consumption rate of *Drosophila* was $2\frac{1}{2}$ times that obtained by Wigglesworth in closed vials. Probably the movement was responsible for this, although Weis-Fogh (1952*a*) found no difference in the metabolic rates of tethered locusts and those flying on a roundabout.

From the connected values of fuel consumption and air speed taken from these curves, values for the efficiency over this range of speed were calculated from the expression,

$$e_o = \frac{\frac{M^2 g^2 t}{2m} + Rd}{E} \quad . \quad . \quad . \quad . \quad . \quad (6)$$

where R is the distance flown in the time t, d the drag at this speed (R/t), and E the energy value of the meal. Curves connecting these values with the speed of flight were then drawn (figs. 22 to 26). Extrapolations are indicated by broken lines on all curves.

For all species there appears to be a basic minimum rate of fuel consumption necessary to maintain the insect in the air. There is very little increase above this level up to low cruising speeds of flight, but fuel consumption increases very steeply at the higher speeds. The efficiency is a maximum for all species at a low cruising speed, slightly lower at zero speed—i.e., in hovering flight. It decreases rather more rapidly at increasing speeds, in such a manner that it tends towards zero at about the maximum speed recorded in short bursts. The increase in fuel consumption above the basic level is approximately proportional to the cube of the speed at low cruising speeds, where the change in efficiency is slow. At lower speeds the efficiency is increasing and the fuel consumption increases less steeply than the cube of the speed. At higher speeds the efficiency is decreasing and the fuel consumption grows more rapidly than the cube of the speed.

3. FLIGHT BEHAVIOUR.

Incidental to these studies on efficiency the flight mills permitted many observations on flight behaviour—a subject in the study of which this equipment offers great possibilities. These observations may be summarized by species as follows :—

T. affinis.—On coming round from anaesthesia and finding itself attached to the needle this insect would start to fly, and would repeatedly jerk the left wing forward and the right wing back, and vice versa. This was interpreted as an attempt to steer itself off the arm, and was continued whether the insect were stationary or moving. After four or five flights memory of the significance of the landing mushroom was apparent. When nearing exhaustion the insect would momentarily adopt a grappling attitude with the legs spread out (Pl. VI) every time it passed over this position. Most flies showed a periodical speed variation, bursts of high speed lasting ½ to 1½ minutes alternating with periods of slower flight lasting about twice as long. Flight could only be initiated at temperatures above 50° F. The rapidity with which glucose meals could be utilized was astounding ; exhausted insects could resume flight within 10 sec. after dipping the proboscis into a 25 per cent. solution. This may be a general characteristic of flying animals ; Pesserl (1939) demonstrated that nutriment passed through the gut of a canary three times as fast as through that of a mouse. *T. affinis* was the easiest insect to work with, of a convenient size, and nearly every specimen flew and fed readily and gave sharp end-points.

T. septentrionalis.—Similar to *T. affinis* in many respects, but the slower intervals too often ended in flight stopping altogether, usually over some conspicuous object. This could be prevented by covering the eyes with indian ink, when absolutely uniform speed at an intermediate level usually resulted.

Chrysops nigripes, *C. furcata*, *C. carbonaria* Wlk. and *C. frigida* O. S.—None of these species flew continuously on the mills or on threads. Covering the eyes, with or without the ocelli, effected no great improvement. Flight was fast while it lasted, which was never for more than a few minutes at a stretch. There are no records of long flights by this genus in nature.

Aëdes nearcticus was the best of the mosquitoes, but *Aëdes flavescens* and *A. punctor* also flew well. *A. communis* was the worst flier of all the species tested. Feeding difficulties with mosquitoes have already been mentioned. Specimens taken early in the season yielded the highest proportion of good fliers. Intermittent flight was obtained at temperatures down to 36° F., twelve degrees lower than for any other species. All the mosquitoes here fly at night, none of the tabanids or black flies. Only the mosquitoes have dorsal oesophageal diverticula. The position of these, in the anterior lateral angles between the two sets of indirect flight muscles and close up against these, suggests that in spite of the proven impermeability of the ventral diverticulum, these may supply glucose directly to the flight muscles at low temperatures. If so, Eysell (1907) was more correct than he realized when he named these structures *Flugblasen*.

Simulium venustum and *S. vittatum*.—Flew and fed well, particularly early in the season. The failure of many later specimens was associated with a diseased condition. Several specimens, after flying in a circle for some time, increased the amplitude of the movement of the inner wing, and decreased that of the outer wing. One of these was reversed on the arm, when the differential amplitude was also reversed, suggesting that this represented an attempt to steer out of the circle enforced by the mill. Intermittent flight could be obtained at temperatures down to 48° F., and continuous flight down to 55° F.

Apis mellifera.—As expected from the observations of Fraenkel (1932), the bee proved a difficult insect, largely because of the habit of tucking the abdomen forwards between the tarsi and then refusing to fly. No differences were found in the performances of field bees collected in the field or at the hive and home bees. Possibly bees taken from a swarm would be more satisfactory. The best results were obtained with bees which had been separated from the colony and fed sugar syrup in a cage in the laboratory for at least a week. Like *Simulium*, the bee showed differential amplitude of wing beat, and reversed this when it was reversed on the mill ; this was so marked with one specimen that the vibration of the outer wing actually ceased altogether at intervals. Betts (1931) dismissed steering by differential amplitude in the honey bee as impossible. Removal of various combinations of tarsal segments did not effect sufficient improvement in performance to offset the complications which it would introduce ; blackening the eyes and ocelli also had little effect. Many of the bees which flew appeared to be making prodigious efforts to travel in some other direction than that which was forced on them. This is reflected in the erratic distribution of the points in fig. 25. Bees learned the position and significance of the landing mushroom very quickly, and often before completing a single flight would not merely grapple for this on each circuit, but would momentarily stop flying. End-points, when they could be reached, were sharp.

Drosophila.—In view of previous work *Drosophila* was expected to be easy to handle. This proved wrong, and great difficulty was at first experienced in getting it to fly more than a few consecutive revolutions. Chadwick (1939*a*, 1947) and Wigglesworth (1949) had no difficulty in getting continuous stationary flight from *Drosophila.* On a mill there are the additional stimuli of increased air flow, and movement of the visual field. It proved to be the latter, particularly below the insect, which was inhibiting rather than stimulating flight, the flies apparently attempting to alight on any object which came into view below them. When a uniform surface—a white or a black card—was placed below the mill arm flies behaved excellently, at least when flying out on stored reserves. When two or three pieces of contrasting card, each about a square inch in area, were placed on the uniform background, flies came to rest over one of them after two or three revolutions. When these were removed, flight was resumed spontaneously. End-points were not so sharp as with the nematocerous flies, and flights on glucose meals were rather less satisfactory than the preliminary flights. Flies were all between 1 and 5 days of adult age ; the younger specimens were the more satisfactory. The speeds both of individuals and of the group studied were much more uniform than those of any other species. This made it difficult to obtain an adequate spread between the readings.

All species flew faster when some conspicuous object was made to overtake them ; use could be made of this to obtain a better range of speeds from a given number of flights by arranging a background pattern which could be rotated at any selected speed. Better performance was nearly always obtained when there were two specimens flying at the same time. For all species the dominant stimulus for flight was lack of tarsal contact. In the mosquitoes air movement was next in importance, but visual stimulus was more important than this in the bee and *Drosophila.* In the tabanids and black flies these two stimuli were about equal in importance.

To permit comparison with data which have already been published on the rates of energy transformation in flying insects, summarized in Table XI, the

TABLE XI.—*A summary of published information on the metabolic rates of insects at rest and in flight.*

Species.	Metabolic rate (c.c.O_2/gm./hr.). At rest.	In flight.	Author.
ORTHOPTERA :			
Schistocerca gregaria	0·63	10–30	Krogh and Weis-Fogh, 1951
	.	†9·5–28·5(45)*	Weis-Fogh, 1952*a*
ODONATA :			
Aeschna sp.	.	†64(139)	Axenfeld, 1911
LEPIDOPTERA :			
Colias edusa	.	†96(139)	,, ,,
Thais cassandra	0·402	216	Raffy and Portier, 1931
	0·80	24	,, ,, ,, ,,
Deilephila elpenor	0·166	6·2	Kalmus, 1929
Vanessa	.	30	Krogh and Zeuthen, 1941
Unspecified	.	30–500 × resting	Raffy, 1936
DIPTERA :			
Lucilia sericata	.	95·58(187·5)	Davis and Fraenkel, 1940
Musca vomitoria	.	†60(103)	Axenfeld, 1911
Drosophila repleta	1·68 (2·74)	21(29·9)	Chadwick and Gilmour, 1940
	.	14 × resting	Chadwick, 1947
D. melanogaster	1·96	.	Kucera, 1934
	2·37	.	,, ,,
D. melanogaster	.	†12·4(21·7)	Wigglesworth, 1949
HYMENOPTERA :			
Apis mellifera	3·23	(at 14° C.)	Farrar, 1931
	3·76	(at 26° C.)	,, ,,
	0·54	.	Woodworth, 1932
	.	34	Parhon, 1909
	.	†92·5	Lundie, 1925
	.	73	Tauchert, 1930
	.	312 at 18° C.	Kosmin *et al.*, 1932
	1·98	87(100·24) at 21° C.	Jongbloed and Wiersma, 1934
	†1·025	in the hive	Rosov, 1946

* Figures in brackets are maximum values.

† Values calculated from data other than rates of respiratory exchange; details in text.

rates of respiratory exchange equivalent to the observed sugar consumption rates have been calculated and are shown in Table XIIA. The figure for *Drosophila* at the maximum cruising speed is calculated from the highest observed sugar consumption; as already mentioned, higher cruising speeds were obtained on stored glycogen. Many of the figures given in Table XI have been calculated from other units or from the measurement of other manifestations of the energy transformations, and some explanation is needed. The figures given by Wigglesworth (1949) for *Drosophila* are calculated from the sugar consumption, in the same way as those in Table XIIA.

The figures attributed to Axenfeld (1911) are calculated from the work done by the insects, assuming an overall efficiency of 0·035 and utilization of glycogen.

TABLE XIIA.—*The metabolic rates in flight in c.c. O_2/gm./hr., calculated from the sugar consumption.*

	On live body weight.			On flight muscle weight.			
	At cruising speed.			At cruising speed.			
Species.	Mean.	(Max.).	At max. speed.*	Mean.	(Max.).	At max. speed.*	Temp. (° F.).
Tabanus affinis	21·6	(62·9)	210	61·7	(181)	601	63
T. septentrionalis	55·6	(68·5)	.	157	(194)	.	63
Aëdes flavescens	21·9	.	.	.	.	.	60
A. nearcticus	20·6	(58·2)	118	92·9	(272)	559	59
Simulium venustum	27·4	(37·1)	84	114	(156)	358	60
S. vittatum	49·5	(52·8)	.	210	(224)	.	61
Apis	60·5	(97·8)	148 †313	266	(431)	656 †1387	68
Drosophila	32·9	(39·9)	95	134	(163)	396	72

* At the maximum speed in a short burst, by extrapolation.

† At the maximum speed recorded in the field (Park, 1923), by further extrapolation.

No account has been taken of the work against the drag of the mill. Axenfeld did not mention the time taken by the insects to do the work which he measured. Prochnow (1928) assumed this to be one second, and this value has been adopted.

The value for the metabolism of the honey bee in flight, attributed to Lundie (1925), was calculated from the remarkable data given by the author on the numbers of flights from hives in relation to changes in weight. An average nectar concentration of 30 per cent., an average load of 20 mg. and a resting metabolism of 2·5 c.c. O_2/gm./hr. were assumed. This figure is based on 1·275 $\times 10^6$ bee hours of flight. The value of the metabolic rate of the bee in flight given by Kosmin *et al.* (1932) has been questioned (Chadwick and Gilmour, 1940), perhaps rightly; but the maximum speed recorded by Park (1923), requires metabolism of this order (see Table XIIA). Measurements of bee metabolism in the hive have been published by Vansell (1929), but his figures are very low, even if the colonies were exceptionally small. Kalabukhov (1935) has noted a smaller food consumption in bees kept in groups than in those kept singly.

4. RESTING METABOLISM AND NET EFFICIENCY.

The resting metabolism was measured for one species from each family. A microrespirometer adapted from that described by Barth and Kirk (1942) was used. Measurements were made on six single specimens except for the black flies and *Drosophila*; three groups, each of three or four specimens, were used for these. Approximate rates for the other species were obtained by calculation in accordance with the surface law. From these data the maximum value of the net efficiency, which Brody (1945) has defined as the useful work accomplished divided by the (energy equivalent of the) oxygen consumed during the work above that consumed at rest, has been calculated. Allowance was made for the 1 per cent. solution of sugar which apparently cannot be absorbed (Part IV, section 2, a). The results are shown in Table XIIB. There is a general tendency for those insects with the smaller ratio of metabolic rate in flight to that at rest, to show

TABLE XIIB.—*The metabolic rates at rest, the ratio of flying to resting metabolism, and the maximum net efficiencies.*

Species.	Resting metabolism (c.c. O_2/gm./hr.).	Temp. (° F.)	Ratio *flying/resting.	Maximum net efficiency.
Tabanus affinis	0·828	66	26	0·048
T. septentrionalis	*1·13*	.	49	.
Chrysops furcata	*1·52*	.	.	.
C. nigripes	*1·60*	.	.	.
Aëdes campestris	4·47	63	.	.
A. communis	*5·72*	.	.	.
A. flavescens	*3·84*	.	5·7	.
A. nearcticus	*5·57*	.	3·7	0·070
A. punctor	*4·64*	.	.	.
Simulium venustum	†4·41	69	6·2	0·046
S. vittatum	*4·82*	.	10·2	.
Apis	3·16	72	19	0·031
Drosophila	†4·98	77	6·6	0·069

* At the observed mean cruising speed of flight (Table XIIA).

† Measured on groups of flies.

Italic figures are estimates calculated from the experimental figures for other species in the group.

higher maximum net efficiency. This supports the assumption advanced earlier, that most of the difference between the theoretical maximum possible efficiency and that actually found is due to a lower metabolic efficiency. If the aerodynamic efficiency is accepted as 0·66, the highest net efficiency, 0·07, then represents a muscular efficiency of 0·106.

In Table XIIA the metabolism in flight is also expressed in terms of the weights of the flight muscles, which are given in Table XIV. The oxygen consumption equivalent to the maximum observed continuous rate of sugar utilization is about 43 times the maximum continuous rate for human muscle. If the relationship total metabolism $\propto W^{-0.27}$ applies, the maximum continuous rate expected for the honey bee would be about 40 times that of man. The maximum power output, however, probably exceeds that of human muscle by a much smaller factor, since the efficiency is less. For brief periods speeds equivalent to more than three times these values were recorded.

At the beginning of a long-range flight the muscles have to operate at close to their maximum output, and therefore at low efficiency, just to support the heavily laden insect. If it is accepted that the Diptera and Hymenoptera are among the most efficient flying insects, the maximum average overall efficiency at which any insect operates on a long range flight can hardly be more than about 0·05. At the maximum speeds of flight values much lower than this, probably less than 0·01, are to be expected.

PART V.—THE MEASUREMENT OF INSECT FLIGHT RANGE.

1. Methods Employed Hitherto.

The most widely used method of measuring flight range has been that suggested by Pearson and Blakeman (1906); this has been used on the housefly by Jepson (1909), Copeman *et al.* (1911), Hindle (1914), Parker (1916), Bishop and Laake (1921) and by many workers on other species. In the earliest applications coloured blackboard chalk was used as a marker; since then dyes (Zetek, 1913; Clarke, 1937; Dalmat, 1950), vital staining of larvae (Weathersbee and Hasell, 1938), metallic dusts (Majid, 1937; Wallace, 1940; Causey and Kumm, 1948), fluorescent materials (Zukel, 1945; Pal, 1947; Reeves *et al.*, 1948; Polivka, 1949; Thomas, 1951), and radioactive materials (Lindquist *et al.*, 1951, Jenkins and Hassett, 1951; Schoof *et al.*, 1952; Yates *et al.*, 1952) have all been used. Natural marking with distinctive pollen or pollenia of a plant of circumscribed distribution (Marshall, 1872; Shapiro *et al.*, 1944) or with malarial parasites (Kligler and Mer, 1931), and distinctive mutant forms (Burla *et al.*, 1950; Quarterman, 1949) have also been used. This method yields good results so long as the range of flight is rather limited, communications are good, and the insect is readily trapped in large numbers. It is well adapted for studies on most species of *Anopheles* that transmit malaria, and most of the information on the flight habits of these species has been obtained in this way. It breaks down completely where there is a combination of long flight range and difficult terrain. Even under favourable conditions it is rare for as many as 5 per cent. of marked specimens to be recovered—a small proportion on which to base firm conclusions.

A further method which has given much information on flight range is the direct observation of dispersion from known restricted breeding sites. Partly on account of the difficulty of locating all breeding sites, and partly because of the frequent distribution of insects on aircraft, trains and other vehicles, including animal hosts, information obtained in this way is not always reliable. The safest data are obtained when the movement is across the sea or an arm of the sea (MacCreary and Stearns, 1937; Stearns and MacCreary, 1938), or across a river (Drozdova, 1941) or a desert area (Demokidov, 1925; Garrett-Jones, 1950). Reliable information is only obtainable across hospitable land when the larval habitat is quite specific as with salt marsh mosquitoes (Provost, 1951) and some Simuliidae (Rempel and Arnason, 1947).

Qualitative data on flight range have been obtained by Blanton *et al.* (1950) and by Wilson (1951) from observations on the rate of infiltration of insects into an area previously cleared of them by the application of an insecticidal spray. An attempt has been made by Hocking and Richards (1952) to obtain quantitative data, by studying infiltration of adult Simuliidae into an area from which all larval development had been eliminated by insecticides.

There are a few isolated examples of information on flight range of insects obtained in other ways. Richards (1949) found some evidence that the number of hamuli is related to the normal flight range of bees; he cited Rayment (1932) as follows: "I regard the number of wing-hooklets as an infallible guide to the air-range of the bee . . . ."

Wilkinson (1950) has described a flight recorder which can be attached to a bird to enable a study of its migration; such an instrument could possibly be developed for use with insects, but the prospects of recovery would be slim. Finally, Hocking (1948) has suggested the possibility of estimating flight range from a consideration of the energy available to the animal and the rate at which this is used up in flight, and has made a preliminary calculation of the flight range of a mosquito on this basis; Pearson (1950) has used the same procedure in estimating the flight range of the ruby-throated humming bird.

2. Previous Data on the Flight Range of the Groups Studied.

It is not possible to summarize here all the data which have been obtained by these various methods. For groups other than those studied it is sufficient to mention that figures extend from 79 yards for the males of *Culicoides impunctatus* Goet. (Kettle, 1951*b*) to " perhaps over a thousand miles " for *Danaus plexippus* L. (Williams, 1949*a*). It is no accident that the first of these is one of the smallest of insects, and the second is among the larger.

With the exception of the honey bee, there is very little published information on any of the species studied here. The distribution of flight characteristics among insect groups and species is so capricious that caution must be used in drawing general conclusions about a group from observations on one or a few species. The flight range of biting flies is of such general interest because of their disease transmitting propensity that it is considered worth while to summarize published information. Eyles (1944) reviewed the literature on *Anopheles* flight range up to 1944, and gave 160 references. The maximum range which he quoted in this work is 25 km., to a ship at sea, recorded by Wright (1918) for *A. pulcherrimus* Theo. King, in discussing a paper by Curry (1934), suggested that *A. albimanus* may fly at least 32 km., and added that population pressure is the main stimulus " as with *Aëdes sollicitans*." Information on *Anopheles* published since 1944 and on the other biting flies is summarized in Table XIII. Most of the information on the bee takes the form of observations on the reduction in honey yield with increasing distance from forage (Eckert, 1933; Sturtevant and Farrar, 1935; Lunder and Lunder, 1946; Ribbands, 1951, 1952); this is discussed in Part VII, section 2, c. Cherian (1942) found that marked specimens of *Apis indica* travelled 0·6 km. for pollen. Howell and Usinger (1933) found the average duration of flight of drone bees to be 27·34 min. They were never observed to alight during a flight.

Table XIII.—*A summary of published information on the flight range of insect species related to those studied. Except where otherwise indicated, all figures were obtained by the method of release and recapture of marked females.*

Species.	Range in km.	Remarks.	Author.
TABANIDAE :			
Chrysops dimidiata *C. silacea*	> 1·1	.	Davey and O'Rourke, 1951
Tabanidae, unspecified	145	At Rebecca Shoal	Felt, 1928
CULICIDAE :			
Aëdes aegypti	0·8	To Mombasa Island	Wiseman *et al.*, 1939
A. albopictus	0·44	.	Bonnett and Worcester, 1946
**A. campestris*	16	Observation	Rees, 1935
A. cantator	65	,,	Smith *in* Howard *et al.*, 1912
A. cataphylla	4·8	.	Gibson, 1938
A. communis (♀)	1·54	.	Jenkins and Hassett, 1951
(♂)	0·61		
A. dorsalis	>24	.	Gray, 1952
	c.30	Inferred	Dyar, 1929
	35	Observation	Rees, 1935

TABLE XIII.—*A summary of published information on the flight range of insect species related to those studied*—(continued).

Species.	Range. in km.	Remarks.	Author.
A. flavescens	11	.	Shemanchuk, 1952
A. lateralis	>48	Observation	Stage *in* Matheson, 1944
	24	,,	Hearle, 1926
A. leucocelaenus	5·7	.	Causey *et al.*, 1950
A. nigromaculis	<24	.	Gray, 1952
	>48	From breeding site	Dyar, 1929
	3	.	Thurman and Husbands, 1951
A. scapularis	2·4	.	Causey and Kumm, 1948
A. serratus	11·5	.	Causey *et al.*, 1950
**A. sollicitans*	177	On ship at sea	Curry *in* Matheson, 1944
	65	Observation	Smith *in* Howard *et al.*, 1912
**A. spenceri*	> 4·8	From breeding site	Rempel *in litt.*, 1952
A. squamiger	62	.	Aarons *et al.*, 1951
A. sticticus	40–48	Inferred	Gjullin *et al.*, 1950
	8	.	Stage *et al.*, 1937
A. taeniorhynchus	> 9·7	Across Gulf of Paria	Gilyard, 1944
	65	Observation	Smith *in* Howard *et al.*, 1912
	145	Conjecture	Mayer *in* Howard *et al.*, 1912
(♀)	>32	.	Provost, 1952
(♂)	3·2		
A. terrens	5·6	.	Causey *et al.*, 1950
A. trichurus	3·2	From breeding site	Dyar, 1929
**A. vexans* (♀ & ♂)	26	.	Clarke, 1943
	40–48	Inferred	Gjullin *et al.*, 1950
	4–8	.	Stage *et al.*, 1937
	>16	Observation	Hearle, 1926
	>48	,,	Stage *in* Matheson, 1944
	8–13	,,	Rees, 1935
A. vigilax	>32	On ship at sea	Hamlyn-Harris, 1933
Anopheles culicifacies	2·4–2·8	.	Russell *et al.*, 1944
A. freeborni	<42	From breeding area	Rosenstiel, 1947
A. maculipennis messeae	2·4	Malaria incidence	Dukhanina and Smetanina, 1943
	8		
A. minimus	8·65–2·1	.	Ejercito and Urbino, 1951
A. pharoensis	29–45	Observation, wind assisted	Garrett-Jones, 1950
A. pseudopunctipennis	1·45	.	Reeves *et al.*, 1948
	3·2–6·5	.	Levi-Castillo, 1945
A. quadrimaculatus	15	.	Clarke, 1943
	5·9	.	Eyles *et al.*, 1945
A. sergenti	< 8	.	Shapiro *et al.*, 1944
A. sundaicus	3·2	From breeding site	Venkat-Rao *et al.*, 1942
Chaoborus astictopus	9·7	,, ,,	Lindquist and Deonier, 1942
Culex fatigans	3·2	,, ,,	Afridi *et al.*, 1938
	2·4	.	Reeves *et al.*, 1948
**C. pipiens* (♂ & ♀)	23	.	Clarke, 1943
C. stigmatosoma	1·6	.	Reeves *et al.*, 1948
**C. tarsalis*	4	.	,, ,, ,,
	1·6	.	Thurman and Husbands, 1951
Culiseta incidens	0·61	.	Reeves *et al.*, 1948
C. inornata	26	.	Clarke, 1943
Haemagogus spegazzinii	11·5	.	Causey *et al.*, 1950
**Mansonia perturbans*	several	Observation	Matheson, 1944
Psorophora confinnis	14·5	,,	Horsfall, 1942
Mosquitoes, unspecified	154	At Rebecca Shoal	Ball, 1918

TABLE XIII.—*A summary of published information on the flight range of insect species related to those studied*—(continued).

Species.	Range in km.	Remarks.	Author.
SIMULIIDAE :			
Prosimulium hirtipes	3·2	Reoccupation of cleared area	Hocking and Richards, 1952
Simulium arcticum	16–19	Observation, wind assisted	Cameron, 1922
	160	Ditto	Rempel and Arnason, 1947
S. callidum	12	.	Dalmat and Gibson, 1952
S. reptans columbaczense	145	Observation	Baranov *in* Rempel and Arnason, 1947
**S. damnosum*	> 0·92	From breeding site	Kirk, 1947
	72	Suggested	Gibbins, 1936
	35	From breeding site	Wanson, 1950
**S. griseicolle*	320	Suggested	Edwards *et al.*, 1939
	>80	From breeding site	Lewis, 1948
S. luggeri	42	.	Fredeen *et al.*, 1953
S. metallicum	1·6–16	.	Dalmat, 1952
S. nigroparvum	10–16 in large numbers	Observation	Underhill, 1938
	24 in small numbers	.	
S. ochraceum	3·2	.	Dalmat, 1952
	10	.	Dalmat and Gibson, 1952
S. ornatum	1·6	From breeding site	Edwards, 1920
S. venustum	3·2	.	,, ,,
	9·7	Reoccupation of cleared area	Hocking and Richards, 1952
Simulium sp.	32	Observation, wind assisted	Webster, 1902
	>12	.	Dalmat, 1950

* Observed feeding at flowers ; see Table II.

3. RESULTS OBTAINED BY THE INTRINSIC METHOD.

The precise calculation of the flight range from the data available is complex since neither constant power, constant speed nor constant efficiency can be assumed. Breguet's formula (Durand, 1934 ; Von Mises, 1945), which is used to solve a similar problem for aircraft, cannot therefore be applied. At the start of a flight which may attain maximum range the muscles are working at close to their maximum power, and only a very low speed is possible. It has already been indicated (Part II, section 2, b) that the load which these insects can carry is limited both by the capacity of the crop and the thrust which can be exerted by the wings. This was confirmed by calculations on the data in sections 3 and 4, which indicate for all species that the mean maximum load (Table III) is just within the lifting power of the insect. The absolute maximum loads are mostly beyond the average lifting power, indicating that the specimens which gave these figures were exceptional as regards muscular power as well as crop size.

The work done on a flight of distance R is the product of the distance and the parasite drag plus the product of the mean power required for support and the time of flight, $\frac{R}{V}$, where V is the speed. This work done is equal to the product of the energy available and the average efficiency. That is:

$$Rd_p + \frac{R}{V} \cdot \frac{M^2g^2}{2m} = Ee_o,$$

whence $$R = \frac{Ee_o}{d_p + M^2g^2/2mV,} \qquad (7)$$

or, in full $$R = \frac{Ee_o}{\rho C_D S V^2/2 + M^2g^2/V.8k\rho.Al\theta n}. \qquad (8)$$

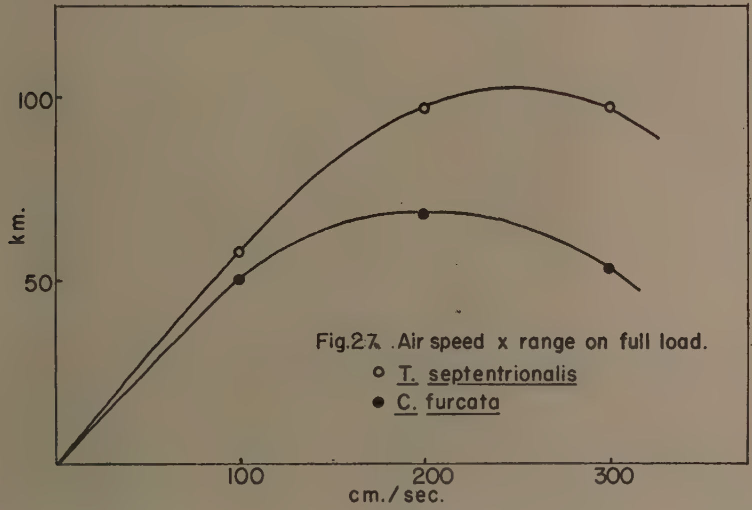


FIG. 27.—The relationship between air speed and range on full load, *T. septentrionalis* (above), and *C. furcata*.

By solving this equation for a series of values of V it is possible to draw a curve connecting R and V (fig. 27), which shows a maximum value for R at a low cruising speed of flight. But to do this it is necessary to decide on appropriate values of M and e_o.

If the load is small, the average of the initial and final values of M gives a good approximation. To decide the best value for these larger loads, the ranges of *T. affinis* on various speed programmes were first determined graphically. The power requirements at each speed at hourly intervals from the start of a flight with full load were calculated. These values were used to draw curves connecting the weight of the insect with the time for which it had been flying, for each speed programme, from which the range was obtained (speed × time). The shape of these curves suggested that if the basic weight plus one-third of the maximum load were used for M in equation 7, this would give a good approximation to the range at the lower speeds. This value was tried and gave results in good agreement with those obtained graphically. This procedure was repeated for *A. nearcticus*, for which the values obtained graphically and by approximate calculation also agreed well.

For the overall efficiency, an average of the values at the maximum recorded consumption rate and at the basic weight and the appropriate speed was used.

Typical curves connecting range and speed are given in fig. 27. The maximum values of the range, and the speeds at which these would obtain, are given in Table XIV, columns 1 and 2. A rough check on these figures for range was obtained directly from the flight mill data (Appendix C). This was done by plotting the flights on a graph, with total distance as the abscissa and consumption (mg. sugar fed) as the ordinate. A line was drawn parallel to the abscissa to represent the amount of sugars contained in the mean full load plus the tissue reserves (Table III), and a curve was drawn through the points and extrapolated to cut this line. The resulting figures for range are given in Table XIV, column 3, and a typical curve is shown in fig. 28. The values are lower than those obtained by calculation by amounts which vary with the differences between the mean speeds on the mills and the optimum speeds. Thus the two figures are nearly the same for the bee, which flew very slowly on the mill, but differ quite widely for *Drosophila*, which flew fast.

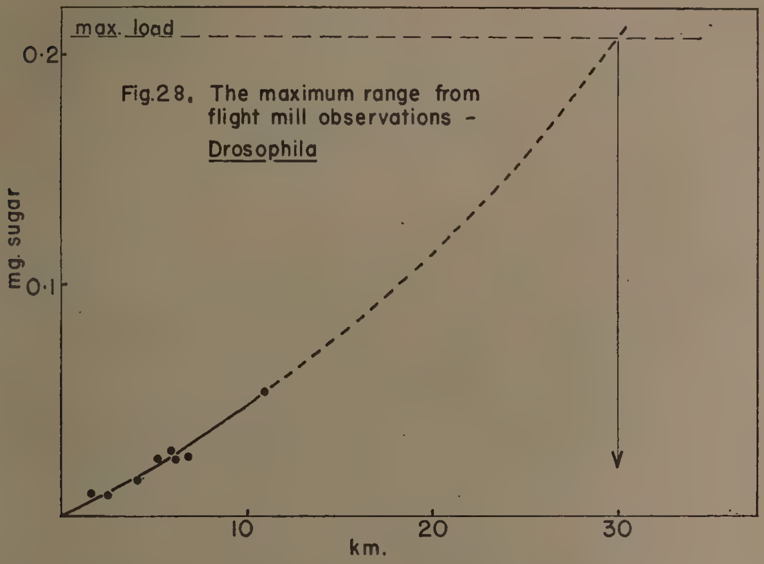
TABLE XIV.—*The range of flight and the endurance of the species studied.*

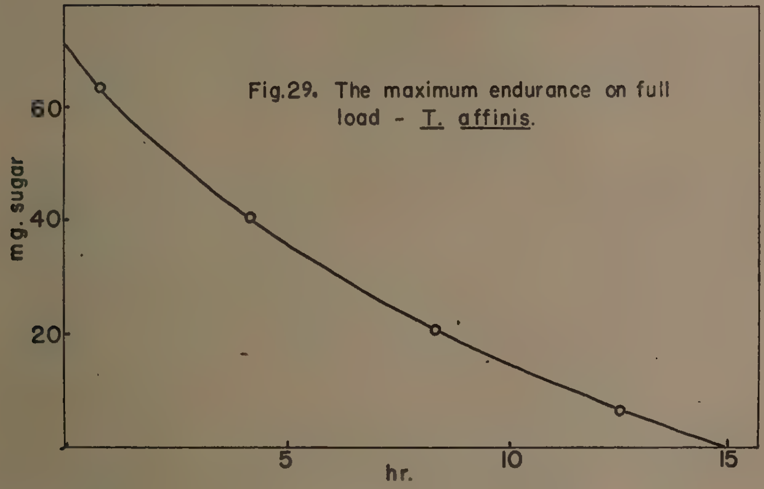
Species.	Calculated max. range (km.).	Required speed (cm./sec.).	Range from mill data (km.).	Maximum endurance (hr.).
Tabanus affinis	99	270	91	16
T. septentrionalis	102	250	.	17
Chrysops furcata	69	210	.	15
C. nigripes	76	210	.	16
Aëdes campestris	53	115	.	22
A. communis	22	120	.	7
A. nearcticus	48	110	40	22
A. punctor	46	120	.	20
Simulium venustum	116	125	102	35
S. vittatum	104	115	.	34
Apis	46	250	44	7
Drosophila	48	100	30	14

The mean maximum range of the insects composing the swarms of females described in Part II, section 2, c has also been calculated from formula 7. The mean value for the three swarms of *Aëdes punctor* is 19 km., that for *S. venustum* is 45 km., and that for *S. vittatum* 75 km. It may be supposed that when the light becomes too weak to permit visual orientation to the conspicuous object over which the swarm formed, continuous flight in one direction supervenes.

To illustrate the general application of this formula for flight range, the expected maximum range for insects from two other groups were calculated. A migrant butterfly and a locust were chosen, both of them larger than any insects studied in this investigation. Because adequate data are not available for any one species, composite data on *Danaus plexippus* L. (fat content, Beall, 1948) and *Vanessa antiopa* L. (dimensions, Sotavalta, 1947) were used. For

Schistocerca gregaria Forsk. the data given by Weis-Fogh, 1952, and Kennedy, Ainsworth and Toms, 1948, were used, and the sectional area of the thorax was taken from *Schistocerca serialis* Thun. Adjustments were made for size differences, and a water content of 60 per cent. at full fat load was assumed in





FIGS. 28–29.—(28) The maximum range derived from observations on the flight mill. *Drosophila*. (29) The maximum endurance on full load. *T. affinis*.

converting from Beall's dry weight percentages. k was taken as 1·9 for both species; C_D as 1·1 for *Vanessa-Danaus* and as 1·12 for *Schistocerca*; the overall efficiency used was 0·05. The data used were as follows:

	Basic. wt. (g.).	A (cm.^{2}).	l (cm.).	θ (radians).	n (cycles/ sec.).	S (cm.^{2}).	E (ergs).
Danaus-Vanessa	0·354	20·3	3·8	2·1	10	0·3	$7{\cdot}0 \times 10^{10}$
Schistocerca	2·0	29·8	6·0	1·92	20	1·16	$1{\cdot}26 \times 10^{11}$

and the results obtained for the maximum flight range:

Danaus-Vanessa . .	1050 km. at 250 cm./sec.
Schistocerca . . .	350 km. at 275 cm./sec.

It is thus necessary to postulate only a very modest following wind to explain the presence of the monarch butterfly on oceanic islands more than a thousand miles from its origin, and the passage of *Vanessa cardui* from Australia to New Zealand (Williams, 1949*a*). The presence of *Schistocerca* 370 miles from land (Darwin, *in* Wallace, 1876) is equally readily explained. The figures given by Weis-Fogh (1952*b*) for the endurance and speed of *Schistocerca* indicate a maximum flight range of 330 km.—rather less than the above figure, but the speed of his specimens was higher, 420 cm./sec. The range at this speed from my curve of range × speed would be 300 km. No account has been taken in these calculations of the possible limiting influence of water requirements.

The only insects likely to be able to exceed this range are those which, like the dragonflies, are able to feed on the wing. It is possible that such insects could maintain themselves in flight for very much greater times and distances on the food material which they could pick up from the aerial fauna. If any insect flying on fats had flight muscles of the proportions of, say, *T. septentrionalis*, it might well carry enough fuel to double this range if the water problem could be solved.

4. ENDURANCE.

Of particular interest in connection with the influence of wind on insect dispersal is the maximum time for which an insect can maintain itself in the air. This is readily arrived at for the species used in this study by a graphical procedure similar to that used for the range; an example is given in fig. 29. The results obtained are included in Table XIV. A useful approximation to this figure is given by calculation as follows. The fuel consumption required to support the insect is calculated, (*a*) when it is fully laden, and (*b*) when it is exhausted. These values are divided into the total fuel load to give the endurance at each consumption rate. The endurance at full load, plus one-third of the difference between this and the endurance at the basic weight, is approximately equal to the endurance obtained graphically.

The average endurance of the specimens of *Aëdes punctor* collected from three swarms of females (Part II, section 2,c) calculated by this method comes to 12 hours. The corresponding figure for *S. venustum* is 19 hours, and for *S. vittatum* 25 hours.

It is clear from these figures, and the speeds of flight recorded in the next section, that the contribution which wind may make to the dispersion of insects is potentially greater than that which insects may make by their own efforts in flight.

5. Discussion.

The relationship between the maximum flight range of insects and their size is not a simple one. It might be expected that the range would increase with increasing size, and up to a point this appears to be so among insects of similar construction. As the size approaches the limit at which flight becomes impossible, a reduction in the range must be expected. In the formula for flight range (8), the energy which an insect may carry was shown in Part III, section 3, to vary with the linear dimensions as $a\underline{L}^{2\cdot19}-\underline{L}^{3\cdot2}$; the overall efficiency appears to be independent of size. In the denominator the first term varies as $\underline{L}^2$ and the second approximately as $\underline{L}^{3\cdot2}$ (Part III, section 3). The range should therefore vary as: $\frac{a\underline{L}^{2\cdot19}-\underline{L}^{3\cdot2}}{\underline{L}^2+\underline{L}^{3\cdot2}}$ or as: $\frac{a\underline{L}^{0\cdot19}-\underline{L}^{1\cdot2}}{\underline{L}+\underline{L}^{1\cdot2}}$. This expression represents a curve which increases with $\underline{L}$ while this is small, reaches a maximum and then decreases again. There is so much variation in the proportion of wings and muscle weights to body weight that it is not possible without much more extensive data to deduce the size of insect at which the range would be a maximum. This would be different in the different groups. It is likely that the monarch butterfly, so well adapted to long flights in other ways, would prove to be close to the optimum size for insects flying on fats, with a low wing-loading and low frequency.

All the flight distances recorded in Table XIII are compatible with those of which related species are physiologically capable if assisted by following winds of less than average speeds.

PART VI.—THE MEASUREMENT OF THE SPEED OF INSECT FLIGHT.

1. Review and Methods Employed.

There is little reliable information on the speed of flight of insects. Even that on the speed of birds, which is easier to measure, is quite limited. There are many estimates of speed, but these are usually greatly in excess of actual speed for both birds (Cooke, 1933) and especially for insects. Much conflicting information could be resolved if all observers distinguished between air speed and ground speed, and gave data on wind speed and its direction relative to flight direction. Speeds in a dive may of course be much higher than those in level flight, particularly for large animals, and level flight in an upward current of air is, from this point of view, a dive. Probably few birds regularly exceed an air speed of 100 m.p.h. except in a dive (Meinertzhagen, 1921). As Aristotle pointed out, the flight of insects is slow and weak by comparison, although there are estimates to the contrary. Most of the more reliable observations place the maximum speed of insect flight at about 35 m.p.h., although Hankin (1914) has reported 36–48 m.p.h. for dragonflies, and Tillyard (1917) has recorded about 58 m.p.h. for the dragonfly, *Austrophlebia*, wind speed and direction unspecified.

Methods which have been used for measuring the speed of insect flight include : direct timing in the open with a stopwatch (Demoll, 1918 ; Park, 1923); similar timing under various controlled conditions, such as flight towards a window in a room, or towards a light at the end of a tube (Demoll, 1918 ; Bentley, 1914) ; observations in a wind tunnel (Kennedy, 1939) ; comparison with the speed of a train or other vehicle (Twinn *et al.*, 1948 ; Nielsen and Nielsen, 1950 ; Fernald, 1925). Magnan (1934) harnessed insects to a thread wound on a light drum, the revolutions of which were recorded on a kymograph, and also suggested cine-photography against a grid. Schnell-Larsen (1934) used an ingenious photoelectric method ; the flying insect successively interrupted the two segments of a beam of light which was reflected twice through a tube, and on to a photo cell. The distance between the segments of the beam was known, and the interval between the interruptions was measured electrically.

The only estimate of insect flight speed that needs mention is that of Townsend (1926, 1927, 1939), which placed the speed of *Cephenemyia* at 400 yards per second (820 mi./hr., 36,600 cm./sec.). It was the refutation of this estimate on physical grounds by Langmuir (1938) that suggested the approach to insect flight range and speed used in this study.

2. PREVIOUS DATA ON THE SPEED OF THE GROUPS STUDIED.

These data are summarized in Table XV. Much speculation and many observations have been made on the flight speed of the honey bee. Estimates as high as 120 m.p.h. have been made, although most conservative observers

TABLE XV.—*Summary of published information on the speed of flight of insects related to the species studied.*

Species.		Speed (cm./sec.).	Method.	Author.
Tabanus bovinus		<1400	Stopwatch ; flight in a room and outside.	Demoll, 1918
T. bovinus		400	Attached to a thread	Magnan, 1934
T. affinis		<1250	Comparison with train	Twinn *et al.*, 1948
Tabanids (*unspecified*)		>1800	Comparison with car	Schwardt, 1932
Aëdes aegypti		150	When forced by wind	Kennedy, 1939
		30–40	Otherwise	,, ,,
Anopheles fuliginosus *Mansonia uniformis*		8–33	Towards light along 25 ft. tunnel	Bentley, 1914
Apis workers	Av.	612	Stopwatch in field over 1/5 mile	Park, 1923
	Max.	*800		
	Av.	375	Stopwatch in field over 3 metres	Demoll, 1918
	Max.	600		
	Av.	556	.	Beutler, 1950
		250	Attached to a thread	Magnan, 1934
		600	.	von Frisch, 1927
		830 empty	.	Hansson, 1945
		720 full	.	.
Apis drones		180	Photoelectric method	Schnell-Larsen, 1934
Drosophila spp.		420	.	Weis-Fogh, 1952*b*

* 1120 cm./sec. also recorded but distance not given, and no clear indication whether this was corrected for wind speed.

have given a figure below 30 m.p.h. (Park, 1923). The earlier observers took no account of wind speed. Park's figures (1923, 1928*a*) are the result of careful timing of marked bees in the field with a stopwatch, combined with observations on wind speed and direction. He found that air speeds were higher when bees were flying against the wind, indicating visual compensation. The maximum speeds of loaded bees returning to the hive were less than those of bees going out empty, but the average speeds of the loaded bees were higher, perhaps because their flights were more direct. Demoll (1918) and Hansson (1945) also found a lower maximum speed for loaded bees. Demoll's measurements were made over a 3 metre stretch from 2 metres in front of the hive up a slope of about 20°. In spite of this, unlike Park, he found lower speeds on the return flights than on the outward flights. Possibly this was a fatigue effect, since in his method return flights were measured at the end of the trip, outward flights at the beginning.

There is no published information on the speed of black flies. Dalmat (1950) in his studies on flight range found one female of *Simulium metallicum* Bellardi 3·8 miles from the release point on the following day. With *Drosophila*, Burla *et al.* (1950) found a distribution of 100 metres in one day.

Tabanids have a reputation for fast flight. Twinn *et al.* (1948) reported that *T. affinis* lost ground only slowly when in pursuit of a train travelling at about 30 m.p.h., there were no observations on wind speed, and the flies may have been utilizing air currents drawn along with the train. It seems possible that these flies can overtake their preferred mammalian hosts, many of which attain speeds of about 30 m.p.h., but the figures obtained in this work hardly support this suggestion.

3. THE EXPERIMENTAL MEASUREMENT OF FLIGHT SPEED.

The flight mill experiments gave information on the cruising speeds in continuous flight and the maximum speeds over short distances for some species. The intrinsic approach was used to estimate the probable speeds of flight of the other species studied. The weights of the flight muscles were determined for all species. The specific power output of the flight muscles at cruising and maximum speeds was calculated for the species for which the speed was known from the flight mill work, with the aid of the data in Parts III and IV. It was assumed that within each family, given an equal percentage of muscle, the total power varied as $W^{0\cdot73}$, i.e. that the specific power varied as $W^{-0\cdot27}$. The speeds of which the other species were capable were then estimated by calculating their power output under cruising and short-burst conditions, and finding the speeds to which these were equivalent from the graphs in figs. 13–16. The speeds thus apply to the insects at their basic weights.

Most of the measurements of muscle weight were made by dissecting freshly killed specimens after a momentary exposure to live steam. The specimens and the muscles from them were weighed on a torsion balance. Left and right halves of the larger species were weighed separately, and readings were rejected if the two halves differed by more than 5 per cent. Some of the northern material was dissected after preserving in alcohol-glycerine; the values obtained were substantially the same as those for fresh material of the same species. Only the indirect muscles, the tergo-sternals and the longitudinal median dorsals, were used. The results are summarized in Table XVI.

Table XVI.—*The weights of the indirect flight muscles.*

Species.	Mean weight of longitudinal median dorsal muscles (mg.).	Mean weight of tergosternal muscles (mg.).	Mean total weight of indirect flight muscles (mg.).	Ratio (lmd/ts).	Total flight muscle weight as per cent. basic weight of insect.
Tabanus affinis	28·1	20·9	49·0±4·1	1·34	34·5
T. septentrionalis	10·3	8·68	18·98±3·0	1·19	35·1
Chrysops furcata	4·40	3·22	7·62±0·5	1·36	22·9
C. nigripes	2·73	2·23	4·96±0·3	1·22	26·4
Aëdes campestris	0·456	0·408	0·864±0·11	1·12	16·5
A. communis	0·228	0·202	0·430±0·13	1·13	17·6
A. nearcticus	0·238	0·203	0·441±0·04	1·17	18·0
A. punctor	0·444	0·401	0·845±0·15	1·11	18·7
Simulium venustum	0·271	0·287	0·558±0·14	0·945	23·2
S. vittatum	0·202	0·248	0·450±0·13	0·815	23·0
Drosophila	0·075	0·055	0·130±0·012	1·36	23·7
Apis	9·39	9·45	18·84±1·6	0·993	22·5

Included in Table XVI also is the ratio of the weight of the longitudinal median dorsal muscles to that of the tergo-sternals. There has been some discussion (Osborne, 1951) regarding the relative amount of power used on the up and down strokes of the wings. Since the longitudinal median dorsals and tergosternals are responsible for the down and the up strokes respectively, it seems likely that the ratio of their weights will express this relationship. The highest value of this ratio is 1·36 for *C. furcata* and *Drosophila*, suggesting that about one-third more power may be required on the down beat than on the up beat in these species. For three species, all of them good fliers, the ratio is less than 1. The average value for the group is 1·15. The muscle weights expressed as percentages of the basic weights are naturally higher than those given by other authors, who have used the average weights of the insects as reared or captured. Thus Chadwick and Gilmour (1940) gave 18 per cent. for *Drosophila*, and Weis-Fogh (1952) gave 17 per cent. for the honey bee. All the figures given by Magnan (1934) and Magnan and Perrilliat-Botonet (1932) are lower than those of other investigators. The figure of 35·1 per cent. of the basic weight for *T. septentrionalis* appears to be as high a value as has been reported for any insect.

For the mosquitoes at cruising speed the margin of power above that required to support them in the air was so small that the cruising speeds could not be obtained very closely from the graphs of power × speed (fig. 15). The calculated power to remain airborne (Table IX) was therefore subtracted from the power available, and the surplus power was used to arrive at the speed by trial and error from the drag × speed curves in fig. 11. This difficulty may have arisen because *A. nearcticus* shows an unusually low specific power for a mosquito, and was thus an unfortunate choice for the flight mill work. Alternatively, the value obtained for the specific power of this insect may be rather low.

The results of these calculations are given in Table XVII. For two species a check on the results is provided by direct observations on the flight mills.

For *T. septentrionalis*, although it only weighs about one-third as much as *T. affinis*, the agreement is good both for cruising and maximum speeds. For *S. vittatum* the agreement is fair for the maximum speed but poor for the cruising speed; this is understandable, since the observations were made on a single specimen, which was evidently an unusually good flier.

Also included in Table XVII are the speeds at which the efficiency curves approach zero (fig. 24). Except for *T. affinis* and the bee, these are rather higher than the highest observed speeds of flight over short distances, and may be taken as approximate indications of the maximum speed possible in a short burst. The bee never flew at its maximum speed on the mill. A comparison with the data in Table XV makes this clear. A much more thorough knowledge of the flight behaviour of this insect will be needed before it will give good results with this technique.

TABLE XVII.—*The speeds of flight. All in cm./sec.*

Species.	Continuous or cruising speed Average.	Continuous or cruising speed (Maximum).	Maximum speed over short distance.	Speed at which efficiency approaches zero.
Tabanus affinis	205	(375)	658	640
T. septentrionalis	269, *260*	(283)	612, *642*	.
Chrysops furcata	. *275*	.	. *640*	.
C. nigripes	. *260*	.	. *585*	.
Aëdes campestris	. *75*	.	. *220*	.
A. communis	. *80*	.	. *250*	.
A. flavescens	*110 .	(159)	252 .	.
A. nearcticus	90 .	(164)	222 .	245
A. punctor	. *78*	.	. *235*	.
Simulium venustum	152 .	(201)	238 .	260
S. vittatum	*248, *165*	(271)	295, *245*	.
Apis	258 .	(352)	418 .	620
Drosophila	142 .	(178)	181 .	190

* Observations on one specimen only.

Italic figures, expected values by calculation from muscle weight; other figures by observation.

4. DISCUSSION ON FLIGHT SPEED.

The power output per gramme of flight muscle per second was calculated for each species flown on the flight mills, at three levels of activity: the first was the average corrected speed of flight on the mill, the second the maximum sustained speed of flight, and the third the maximum speed in a short burst. The power was taken from the curves in figs. 13 to 16 and the results are shown in Table XVIII. An average aerodynamic and mechanical efficiency of 0·7 was supposed. Three additional figures were calculated for the bee at speeds recorded by other observers (Table XV). The highest sustained output apart from the additional figures for the bee was about 6 times that for man (Part IV, section 4).

TABLE XVIII.—*Specific power output of flight muscles at various speeds.*

Species.	Average continuous speed.		Maximum continuous speed.		Maximum speed in short bursts.	
	Speed (cm./sec.).	Power (erg./gm./sec. × 10^5).	Speed (cm./sec.).	Power (erg./gm./sec. × 10^5).	Speed (cm./sec.).	Power (erg./gm./sec. × 10^5).
Tabanus affinis	205	1·64	375	3·53	658	13·3
T. septentrionalis	269	2·35	283	2·64	612	15·2
Aëdes nearcticus	90	1·57	164	3·55	222	6·85
Simulium venustum	152	1·99	201	3·39	238	5·18
Apis	258	3·77	352	5·72	418	8·18
	*570	16·78	*740	33·4	*1120	114·5
Drosophila	142	2·83	178	4·56	181	4·65

* Speed values taken from Table XV.

As a preliminary step to arriving at the maximum speed of flight of which any insect may be capable, a calculation was made for *Austrophlebia*, one of the largest dragonflies. Tillyard (1917, p. 322) reported on this insect as follows :

> " As regards speed, many dragonflies are notoriously swift. *Estimates of the speed of a small object are very apt to go astray.* Of the genera known to me, *Macromia* and *Austrophlebia* are by far the swiftest on the wing. As the latter flies regularly *up and down* small mountain streams, I had an opportunity once of timing it over a measured stretch of between eighty and ninety yards. This distance was covered in three seconds ; so that this dragonfly can fly at the rate of nearly sixty miles per hour ! I doubt if any greater speed than this occurs amongst Odonata." (My italics, B. H.)

In making this calculation all the values adopted were those most favourable to a high speed. The specific muscular power was calculated from that equivalent to the highest reported speed of the honey bee (1120 cm./sec.), which is several times higher than the next highest value. The flight muscles were assumed to make up 35 per cent. of the body weight, also the highest known value ; Magnan and Perrilliat-Botonet (1932) gave only 25·6 per cent. for *Aeschna*. A mechanical and aerodynamic efficiency of 0·7 was assumed. The drag coefficient was taken as 1·0. The area of thoracic section was calculated from a comparison of wing span and body length of available N. American species with those of *Austrophlebia* which were kindly supplied by Dr. A. B. Walkom of the Australian Museum. The value arrived at was 1·2 cm.^{2} These values were substituted in a formula for speed, derived from formula 5, Part III, section 3.

$$V = \sqrt[3]{\frac{2P}{C_D S}}, \quad . \quad . \quad . \quad . \quad . \quad (9)$$

where P is the maximum power available, after allowing for efficiency losses. The term in formula 5 for the power required for support may be neglected in considering maximum speed. The absolute maximum air speed of which this species is considered capable in level flight is 1600 cm./sec. or 36 m.p.h. ; in sustained flight the speed would not be greater than 24 m.p.h. This does not necessarily mean that Tillyard's observation is not reliable ; a following wind, downhill flight and the short distance (850 × body length) taken together could account for the difference in the figures. It is well known that muscle may develop power much greater than normal for very brief periods (Haughton, 1873). It is worth noting that even the great fossil species *Meganeura monyi* with its 29 in. wing span would on a similar basis only have been capable of 43 m.p.h. ; indeed it probably had to fly at close to this speed in order to remain airborne.

It is difficult to see how any insect could greatly exceed these speeds without a profound difference in specific muscular power. The power per unit weight developed by the flight muscles of the bee is so much higher than that reported for other animals that it seems unlikely that any other insect could greatly exceed it. With increasing speed the power required increases very steeply, the efficiency decreases, and any increase in flight muscle weight requires an increase in thoracic section.

PART VII.—GENERAL DISCUSSION AND CONCLUSIONS.

1. MIGRATION, DISPERSION AND EVOLUTION.

The flight range of an insect is of greater consequence in migration than the speed, except in so far as the latter sets limits to the wind speeds against which an insect can make progress, and usually also to the wind speeds at which it will fly at all, at least over land.

Evidence from studies of migration indicates a slight but definite tendency to fly into the wind on the part of butterflies (Williams, 1949*a*), and a rather stronger tendency on the part of locusts (Kennedy, 1951). There is only one account of consistent downwind flights over a period of time and with variation in wind direction (*Melanoplus sp.*, Corkins, 1922). Many authors have recorded movements downwind (e.g., Elton, 1925) without observations on flight direction. Experimental studies of the influence of wind on orientation in flight all indicate a strong tendency to fly into the wind (night-flying Lepidoptera and especially Diptera, Lutz, 1927 ; mosquitoes, Kennedy, 1939). When wind speed is greater than flight speed, locusts tend either to settle or to turn and fly with the wind (Kennedy, 1951), providing ground pattern is visible, so that the insects are aware of their backward movement in relation to the ground. Many insects also show a tendency to start flying as soon after sunrise as their thoracic temperature permits. In general, this means as soon after sunrise as the temperature of land surfaces has been appreciably raised. In the coastal areas around oceans and large lakes the morning on-shore breezes begin to make themselves felt at this time. Inevitably then, these insects tend to fly out to sea (e.g., Pendlebury, 1922). Kennedy (1951 : 192) showed that in flight over water the normal reaction to being driven back by the wind is absent, and he attributed this to the absence of a pronounced visual pattern in the water surface. This may well be correct, but there may be more to it than this. Seen from above the surface of the sea usually appears to be moving in the same direction as the wind. Cornish (1944) has shown that in a steady wind the speed of sea waves is only slightly less than that of the wind. This means that under steady conditions an insect in flight over the sea cannot get the impression of being driven back by the wind, because no matter how strong the head wind, the waves will always be driven back faster than the insect, providing it continues to fly. The stimulus to turn or settle is thus never given. The same principle may also apply to any visible cloud pattern above the insect. In effect, insects flying over water in steady wind conditions can only receive the impression that they are flying in still air, because the air and the visual field tend to move as a unit, with no velocities relative to each other. Whether insects flying out to sea against the morning on-shore breeze will return against the evening off-shore breeze as Pendlebury (1922) observed will depend on the relative strengths of the two breezes, the strength and direction of the overall wind, and the resulting wave conditions.

Insects flying over the sea, whatever the conditions, may be expected to show a strong tendency to continue in a straight line of flight. Waloff (1953) has shown that the flight of the desert locust tends to be more continuous at low saturation deficits. The principal stimuli received by an insect in a swarm or gregarious flight would be those resulting from movements relative to its companions, which would tend to keep the whole swarm advancing on the same course. An individual insect would behave similarly. Only sudden weather changes, shipping and aircraft, the advent of other animals, and either land or exhaustion could change the continuum of effort. The ultimate fate of these insects depends on the relationship between the amount of fuel they carry, and the straight line air distance to land. There may be some sort of " homing reaction " to any object which has motion relative to the wave-air-cloud system, such as a ship, or for that matter an island. This may help to explain some of the peculiarities of island faunas, and the formation and maintenance of swarms may represent a special case of such a reaction.

Oversea flights, even more than those over land, tend to be made against the wind, at least at the outset. This, particularly in view of the meagre speeds of which insects are capable, sets a severe limitation to the widths of sea which may be regularly crossed. These flight reactions must clearly lead to enormous mortality ; yet they have their biological reward in the occasional establishment of a species, in large numbers, in a new area. They are presumably a contributory factor in the formation of insect drifts along the shores of lakes and seas (Criddle, 1931 ; Palmén, 1944).

Aggregation is a very common prelude to migration. It has obvious biological advantages. The music of wing-beat appears to play an important role in this sequence. One insect taking flight stimulates its neighbours to follow (Vayssière, 1921 ; Uvarov, 1928). Physical resonance, arising from specific uniformity of wing-beat frequency, is a strong deterrent to the cessation of flight by any one individual in a crowd of insects. Any individual which does stop beating its wings, before it can close them is stimulated to start again by the hum produced by its companions. This may be why two insects flying at the same time on flight mills, each performed better than one flying alone. It is a decided advantage in favour of the collective mill or roundabout used by Weis-Fogh (1950*a*). Perhaps a vibrator producing the appropriate note would provide useful encouragement for insects reluctant to fly. The swarming flights of termites, ants, and the honey bee suggest that this aggregation-migration sequence may have played a significant role in the development of social life.

Several authors (Heape, 1931; Williams, 1930) have discussed the possibility of starvation as a factor initiating migration, the "alimental migration" of Heape. Unless one regards an insect with an empty gut but abundant fats stored in the tissues as starved, this is hardly possible. A starved insect just cannot migrate. Abundant food supply is a more probable initiating factor.

The literature on migration includes accounts of insects "resting" on ships or on the surface of the sea (Tutt, 1902; Williams, 1930 : 342). In these studies there was no indication that any insect ever stopped flying on account of fatigue as distinct from exhaustion. An exception might be made for *T. septentrionalis*, which showed a tendency to fly very rapidly for a short period, and then to slow down, presumably for respiratory recovery, to an extent which sometimes meant that it would not have been supporting itself in free flight.

It is interesting to note that the insect which showed the shortest range of flight, *A. communis*, is the species in which a new physiological race or perhaps incipient species has been found (Hocking, *et al.*, 1950; Hocking, 1952*c*). Elsewhere regarded as a troublesome biting species (Wesenberg-Lund, 1920; Matheson, 1944), the commoner form at Churchill has not been recorded feeding on blood at all. It apparently uses its flight muscle protein in the development of eggs, thus presumably restricting its flight still further and favouring its isolation and differentiation from the rest of the species. Perhaps the degeneration of the flight muscles in water beetles investigated by Jackson (1952) has a similar significance.

2. The Practical Implications.

(a) *Disease transmission.*—In Part I, section 3g, the expression $PR^2 > 1$, where P is the human population density and R the flight range of an insect disease vector, is given as defining the conditions under which disease transmission becomes theoretically possible. If the data on flight range in Part V, section 3 are substituted in this expression, the following population densities at which these insects become potentially significant are obtained. In calculating these it has been assumed that the normal flight range is a quarter of the maximum possible.

Species.	Persons/square mile.
Tabanus affinis	1/235
T. septentrionalis	1/250
Chrysops furcata	1/114
C. nigripes	1/138
Aëdes campestris	1/68
A. communis	1/12
A. nearcticus	1/55
A. punctor	1/51
Simulium venustum	1/320
S. vittatum	1/260

These figures presuppose that the insects will take two complete or partial blood meals, which has yet to be established for most of these species, and that they are both abundant and efficient vectors. The pathogens which they might transmit have already been briefly discussed (Hocking, 1952*b*). The average population of the Yukon and the North-West Territories at the 1951 census was 1/59 persons per square mile, i.e., sufficient to permit the passage between one human being and another of all these species except *A. nearcticus*, *A. punctor* and *A. communis* in a single flight. It is considered unlikely, however, that significant disease transmission could take place during the short peaks of insect populations without a human population of perhaps ten to twenty times this density. The figures indicate clearly the sequence in which the flies might be expected to become important from this aspect with increasing population: first the black flies, then the tabanids, and finally the mosquitoes.

(*b*) *The pick-up of insecticidal spray.*—The concept of the mass of air passing through the beating wings of an insect per second (Table IX) may prove useful in the study of the pick-up of insecticidal droplets by an insect in flight. The ratio of the amount of spray picked up in flight to that picked up by the resting insect would probably be similar to that of the volume of air passed through the wings per second to the frontal area multiplied by the wind speed. The similarity would be influenced of course by the droplet size of the spray. *Tabanus affinis* passes about 1·9 litres of air through the vibrating wings per second, it has a frontal area of 0·25 cm.^{2}, so that in flight it should pick up spray about 19 times as rapidly as it would when stationary in a head wind of 400 cm./sec. David and Bracey (1946), working with mosquitoes and droplets less than 10 microns diameter, found that the percentage kill of stationary insects increased with increasing wind speed, but that the kill of flying insects was still higher. Kennedy, Ainsworth and Toms (1948), working with locusts and drops of 0·5 mm. diameter, found that the flying insects picked up about twice as many drops as those at rest, but the proportion increased as the drop size was reduced.

(*c*) *Applications in apiculture and biting fly control.*—The fuel consumption of the bee in flight is a matter of some concern to the apiculturist. Phillips (1930) recognized this when he discussed the energy expended in the production of honey, but he was apparently unaware of the data which had already been recorded by Parhon (1909). Beutler (1950*a*,*b*) determined the average fuel consumption, and even demonstrated a correlation between the amount of honey a bee takes from the hive, and the distance of the forage which it visits. Ribbands (1951), however, cited Beutler in support of the view that the effect of the energy used in flying is negligible in considering the reduction in colony weight gains as the distance from the crop increases. The significance of this effect at different nectar concentrations has already been indicated (Hocking, 1952*a*), and can be calculated for the observations of Eckert (1933) and Ribbands. Eckert found that colonies started to lose weight when the distance from nectar sources exceeded 5 miles; i.e., when the round trip distance exceeded 16 km. The sugar consumption per bee on such a trip would be about 6·25 mg. There could be no gain in weight if the average load taken on at the flower (say 25 mm.^{3}) did not contain more sugar than this, i.e., if the nectar concentration were less than about 22 per cent.

By similar reasoning for Ribbands' (1951) data, if the nectar concentration were 30 per cent., about 5·5 per cent. out of the 100 per cent. reduction in yield at $\frac{3}{8}$ mile and 11 per cent. out of the 15 per cent. reduction at $\frac{3}{4}$ miles would have been due to this cause. In the former instance it might be agreed that this factor was negligible if the nectar concentration were more than, say, 60 per cent. A bee consumes its own weight of honey in about 6½ hours' flying, so that at the height of a honey flow a hive with a field force of 2 kg. is using up something like 2 kg. of honey daily in flying, more if it is located at some distance from forage, less if this is close at hand.

In view of the apparent balance between nectar supply and demand in the area studied near Churchill, the introduction of a strong competitor for this vital fuel should restrict the mobility of the biting flies. There are many factors favourable to beekeeping in sub-arctic and tundra areas ; clearly there is abundant nectar, and there is a long working day in which this may be gathered. The principal adverse factor at Churchill is wind. During the main nectar flow in 1947, average wind speed exceeded the maximum cruising speed of the honey bee on 11 days out of 40. In spite of this, inexperienced beekeepers have obtained satisfactory results on a small scale at Churchill and at Dawson City, Yukon. Successful bee-keeping operations have been conducted in the Kola peninsula N. of latitude 67° (Anon., 1951), the Norwegian arctic, the Lofoton Islands, Greenland (Crane, 1952), and Alaska (Pellett, 1920). In Alaska *Rubus Chamaemorus*, *Vaccinium uliginosum*, *Heracleum maximum*, and species of *Salix* and *Achillea*, all of which are represented at Churchill, were utilized for either pollen or nectar or for both, but the bees apparently did not flourish. At the other northern localities results more than met expectations. In view of this, and the fact that bees in adequate numbers might permit tundra species of mosquitoes to be controlled with an aerial spray of 5 square miles instead of fifty, a large scale experiment would appear justified.

No adequate evaluation of aerial spraying techniques against biting flies on true tundra has yet been made. The information on their flight potentialities obtained in this study suggests that this might not even be worth while attempting. To ensure protection for a season from a single application, spraying would have to cover an area proportional to the square of the normal flight range. Assuming this to be one-quarter of the maximum range, as in considering disease transmission, even for mosquito control at least 50 square miles would need to be sprayed, whereas for black flies over 300 square miles would require treatment. Fortunately, black flies are relatively unimportant on tundra, and very low dosages of insecticides applied to selected areas may give good control in the larval stage (Hocking, 1953*a*).

(d) *Aeronautical applications.*—Many authors (Oehmichen, 1920 ; Batault, 1933 ; Melville-Jones, 1929) have suggested that the designers of aircraft can learn much from the study of animal flight. This may be true, but most of these authors refer to efficiency, and in the matter of efficiency the aeroplane is already far ahead of the insect, particularly as regards the power plant. Aerodynamic efficiencies appear to be similar. It is more on the lines suggested by von Holst (1948) and FitzPatrick (1952*a*), in the problems of manœuvrability and stability, that lessons may be learnt from the animal fliers. It is only among a few groups of insects that these powers are well developed. It seems unnecessary to invoke the Katzmayr effect, to set aside the laws of the resistance of the air, or to postulate any mysterious ability to recapture the energy of the vortices they create, to account for the flight performance of insects.

3. Summary of Conclusions.

The range and speed of insect flight are considered from the intrinsic physiological viewpoint, with special reference to 4 northern species of mosquito, 4 tabanids, and 2 simuliids. Confirmatory observations were made on *Apis* and *Drosophila.*

Northern biting flies obtain the energy for flight almost exclusively from floral nectar, of which some flies may carry in their crops quantities ranging up to 217 per cent. of their basic weight.

These nectars contain up to 77 per cent. by weight of sugars, the average concentration on the tundra being 49 per cent., and in the forest 42 per cent. Concentrations of up to 76 per cent. have been found in the crops of the insects studied. The total seasonal production of nectar per acre on the tundra is about 3½ times that in open coniferous forest. The peaks of nectar production on tundra and in forest are synchronous with the peaks of flight of female tundra and forest species of mosquito respectively.

Three of the species found to carry the larger loads of nectar have been observed to form swarming flights consisting of aggregations of females with full crops. These may represent the beginnings of migrations.

Up to about one-third of the lift forces required to maintain these insects in the air is derived from the airfoil action of body surfaces ; the remainder is provided by the resultant reaction of the forces exerted on the air by the wings. The drag coefficients of the insects minus wings, at zero lift, and in terms of the sectional area of the mesothorax, range from about 1·1 for the larger species to 2·3 for the smaller.

The power required to maintain the insects in the air, calculated in accordance with Froude's momentum propeller theory, ranges from 11 erg/sec./mg. basic weight for the smaller species to 38 erg/sec./mg. basic weight for the larger. By mapping air speeds in the slipstreams of two of the larger species, they were found to pass nearly 2 litres of air through the wings per second. The power to overcome parasite drag was measured in a wind tunnel for all species and confirmed for two species on a rotating arm. For all species the power requirement for support equals that for propulsion at a cruising speed of flight.

For all species the overall efficiency of utilization of sugars for flight was a maximum at a low cruising speed, and by extrapolation tended to a slightly lower value at zero speed (hovering), and to zero at maximum speed. Maximum values observed range from 0·029 for *Aëdes nearcticus* to 0·045 for *Drosophila.* At lower speeds the efficiency of *Drosophila* may reach 0·06. The net efficiencies, derived by allowing for the energy required for resting metabolism, reach a maximum of 0·07.

The maximum rates of continuous energy transformation observed range from 803 cals./hr./gm. of muscle for *Simulium venustum* to 2220 cals./hr./gm. of muscle for the honey bee, i.e., from 16 to 43 times the maximum values recorded for human muscle. Speeds equivalent to several times these values were recorded for brief periods. In spite of, or perhaps because of these high rates, power outputs are only about 3 to 6 times those of human muscle ; most of the power loss appears to be in the muscle rather than in the aerodynamic system. The power developed by the different species within each family studied is in broad agreement with the relationship $P \propto W^{0\cdot 73}$. Differences between families mask this relationship.

Values of the average maximum range of flight in still air without feeding extend from 22 km. for *Aëdes communis* to 116 km. for *Simulium venustum.* The maximum speeds in continuous flight extend from about 150 cm./sec. for the mosquitoes to 375 cm./sec. for *Tabanus affinis*. Maximum speeds in a short burst range from 190 cm./sec. for *Drosophila* to 658 cm./sec. for *Tabanus affinis*.

The maximum flight range of any insect unable to feed while flying may be set at about 1000 km. The maximum continuous speed of flight of any living insect is about 12 m./sec., and the maximum in a short burst is about 16 m./sec.

Incidental observations on flight behaviour are included, and the implications of the findings in insect migration, dispersion and disease transmission, and their possible practical applications in aeronautics, apiculture and biting fly control are briefly discussed.

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APPENDICES.

Appendix A.

The body weights, capacities of the crops and concentrations of sugar solutions found therein.

Species.	Weight of insect with full crop (mg.).	Volume of crop contents (mm.^{3}).	Percentage of sugars in crop contents.	Weight of insect empty (mg.).	Load as percentage of empty weight.
Tabanidae :					
T. affinis . . .	224	39·9	68	170·3	31*
	181	21	25	157·8	15
	223	40·8	23	178·3	25
	208	44·8	22	159	31*
	288	92	31	184	57*
	194	29	27	161·8	20
	182	18·1	27	161·6	13
	178	18·7	24	157·4	13
	293	115	22	168	75*
	226	47	29	173	31*
	214	35	25	175·5	22
	171·5	10	69	158	9
	158·4	8	63	148	7
	190	20	76	162	17
	207	42	38	158	31*
	256·5	75	63	159	61*
	170	15·5	72	149	14
	177	18·3	65	153	16
	162	11	60	148	10
	285	103	25	172	63*
	166·7	16·5	32	148	13
	204	45	23	155	32*
	228·6	57	25	162	39*
			Average—	161·7	
T. septentrionalis .	77	6·9	39	69·0	12
	85	5·9	52	78·0	9
	64	8·8	43	53·5	20
	94	13·2	31	79·1	18
	79	11	26	66·9	18
	66	2·7	29	63·0	5
	90	13	30	75·3	20
	149	74	22	69·1	115*
	111	37·4	21	70·6	57*
	74	10·7	49	60·8	22
	77	9·3	38	66·1	17
	96	24·4	40	67·8	42*
	69·4	15·7	44	50·6	37*
	90·4	33·2	48	49·9	81*
	70·1	9·5	34	59·1	19
	69·3	13·5	40	53·4	30*
	53·9	6·7	70	44·8	20
	91·9	32·6	56	50·9	81*
	66·9	9·5	75	53·8	24
	60·7	3·1	57	56·8	7
	64·4	4·1	60	59·1	9
			Average—	61·8	

Appendix A—(continued).

Species.	Weight of insect with full crop (mg.).	Volume of crop contents (mm.^{3}).	Percentage of sugars in crop contents.	Weight of insect empty (mg.).	Load as percentage of empty weight.
C. furcata . .	31·9	7·6	26	23·55	36*
	23·9	*nil*	.	23·9	0
	26·6	1·91	28	24·45	9
	30·7	6·47	25	23·8	29*
	57	3·8	31	41·4	38*
	29·8	0·21	25	29·6	1
	36·8	3·9	27	32·48	13
	25·5	1·18	68	23·95	7
	30·85	0·3	25	30·52	1
	46·2	11·2	30	33·6	38*
	28	1·8	62	25·57	9
	24	2·3	24	21·46	12
	31·2	3·3	67	26·85	16
	30·6	4·6	55	24·67	24*
	25·1	1·5	46	23·3	8
	24·8	0·8	62	23·73	5
	23·5	0·5	54	22·86	3
	33·5	10·2	10	23·0	46*
	27·0	8·5	10	18·3	48*
	28·5	6·2	28	21·6	32*
				Average—26·0	
C. nigripes . .	24·5	2·08	25	22·21	10
	30·6	7·2	25	22·67	35*
	37·0	9·07	24	27·0	37*
	21·3	0·71	25	20·52	3·8
	26·9	3·15	28	23·4	15
	21·9	1·27	30	20·47	7
	32·9	4·85	26	27·57	19
	24·8	5·1	25	19·2	29*
	29·4	4·18	29	24·68	19
	21·8	3·1	47	18·02	21
	38·4	10·3	26	27·0	42*
	24·2	8·4	29	14·7	64*
	21·6	4·1	33	16·92	28*
	29·8	9·2	30	19·4	54*
	21·9	2·6	32	18·94	16
	22·8	3·78	35	18·45	24
	34·2	7·84	35	25·18	36*
	18·7	0·8	48	17·7	6
	20·1	2·1	43	17·6	14
	26·6	2·8	36	23·4	14
	34·0	7·3	32	25·8	32*
	20·9	3·8	38	16·5	27*
	21·1	1·9	32	18·9	11
	30·4	4·0	29	25·85	18
				Average—21·34	

APPENDIX A—(continued).

Species.	Weight of insect with full crop (mg.).	Volume of crop contents (mm.^{3}).	Percentage of sugars in crop contents.	Weight of insect empty (mg.).	Load as percentage of empty weight.
CULICIDAE :					
A. campestris	9·4	1·73	41	7·36	28
	10·6	3·78	28	6·40	66*
	9·95	2·85	27	6·78	47*
	9·2	3·15	29	5·67	62*
	5·7	1·43	30	4·03	40
	9·55	2·27	38	6·92	38
	12·1	1·94	50	9·72	25
	9·05	2·29	62	6·10	49*
	10·7	2·75	21	7·73	38
	8·95	2·85	47	5·47	64*
	7·0	1·22	45	5·54	26
	14·5	4·6	33	9·26	57*
	7·9	1·82	55	5·63	41
	12·75	3·3	60	8·50	50*
	9·0	1·98	55	6·53	38
	8·5	2·55	52	5·29	60*
	10·3	3·15	59	6·24	65*
	9·7	2·05	55	7·13	36
	11·1	2·08	52	8·45	31
	7·35	1·02	60	6·00	22
	9·15	1·8	28	7·15	28
	8·4	2·2	28	5·97	41
			Average—	6·72	
A. communis	4·85	1·20	25	3·53	37*
	3·8	0·61	25	3·13	21
	3·2	0·19	25	2·99	7
	4·2	0·95	25	3·16	33*
	3·9	0·81	25	3·01	30*
	5·3	0·51	23	4·74	12
	5·3	0·89	26	4·32	23*
	3·4	0·37	28	2·98	14
	4·9	1·35	31	3·38	45*
	3·6	0·59	32	2·93	23*
	3·6	0·61	42	2·88	25*
	3·35	0·70	32	2·56	31*
	3·4	0·49	30	2·84	20
	3·1	2·10	36	2·86	8
	3·7	1·11	29	2·44	51*
	3·95	0·94	28	2·91	36*
	3·75	0·54	32	3·14	19
	3·65	0·54	31	3·04	20
	3·45	0·45	28	2·94	17
	3·0	0·34	32	2·61	15
	3·85	0·88	30	2·85	35*
			Average—	3·11	

APPENDIX A—(continued).

Species.	Weight of insect with full crop (mg.).	Volume of crop contents (mm.^{3}).	Percentage of sugars in crop contents.	Weight of insect empty (mg.).	Load as percentage of empty weight.
A. nearcticus	2·9	0·43	25	2·43	20
	3·2	0·52	25	2·63	22
	5·6	2·6	26	2·74	104*
	4·75	1·3	24	3·32	43*
	7·1	3·3	25	3·47	105*
	6·4	2·9	22	3·37	90*
	3·95	0·535	28	3·35	18
	3·75	0·79	21	2·90	29
	3·6	0·64	25	2·89	24
	4·6	0·745	30	3·86	22
	4·8	1·53	29	3·07	57*
	5·4	1·35	29	3·87	40
	4·3	1·06	32	3·09	39
	5·6	1·71	31	3·66	53*
	5·3	1·57	31	3·52	51*
	4·3	0·79	38	3·38	27
	3·85	0·62	35	3·14	23
	3·9	1·1	35	2·64	48*
	5·2	1·36	30	3·66	42*
	3·6	0·85	38	2·61	38
	3·6	0·93	31	2·55	41*
				Average—3·15	
A. punctor	9·6	2·55	28	6·74	42
	9·2	2·45	29	6·45	43
	9·1	1·9	29	5·97	36
	9·75	2·5	31	6·92	41
	9·9	2·6	30	6·17	48
	13·45	5·0	30	7·80	73*
	9·5	3·05	32	6·03	58*
	7·65	1·43	29	6·03	27
	7·5	2·55	29	4·62	62*
	8·0	2·33	27	5·42	48
	9·2	2·9	32	5·92	55*
	7·3	2·2	18	4·90	49
	7·3	3·5	17	3·60	103*
	9·2	2·7	14	6·37	45
	7·9	2·8	35	4·68	69*
	6·9	1·9	13	4·90	41
	12·3	4·2	18	7·80	58*
	7·8	2·6	18	5·05	55*
	8·1	2·8	42	4·80	69*
	8·6	1·8	29	6·56	31
	9·4	4·5	23	4·50	109*
				Average—5·77	

APPENDIX A—(continued).

Species.	Weight of insect with full crop (mg.).	Volume of crop contents (mm.^{3}).	Percentage of sugars in crop contents.	Weight of insect empty (mg.).	Load as percentage of empty weight.
SIMULIIDAE :					
Simulium venustum	4·42	1·32	66	2·68	65*
	5·15	1·58	41	3·29	57
	4·9	1·42	49	3·15	56
	4·3	1·22	50	2·80	54
	4·4	1·23	36	2·96	49
	4·2	0·91	54	3·03	39
	3·5	0·76	45	2·59	35
	6·4	3·6	34	2·27	182*
	6·3	2·9	35	2·97	112*
	5·2	2·4	27	2·52	106*
	5·4	1·8	48	3·18	70*
	5·9	2·8	40	2·62	125*
	4·0	0·9	30	2·99	34
	4·92	2·1	45	2·43	103*
	2·8	0·7	65	1·90	49
	3·3	0·6	73	2·44	35
	2·55	0·5	54	1·91	34
	2·2	0·4	68	1·64	34
	3·04	0·9	76	1·80	69*
	3·55	1·6	55	1·33	152*
				Average—2·53	
S. vittatum	3·1	0·72	42	2·75	38
	3·0	0·55	51	2·32	29
	3·45	0·84	53	2·40	55
	3·75	1·62	30	1·82	100*
	4·2	1·58	32	2·13	98*
	4·05	1·38	43	2·39	70
	3·9	1·17	36	2·55	53
	3·9	1·22	37	2·48	57
	4·2	1·92	32	2·03	107*
	3·8	1·63	26	2·01	89*
	3·9	1·06	29	2·70	45
	3·3	0·92	32	2·28	46
	3·35	1·11	40	2·05	63
	2·62	1·27	38	1·25	110*
	2·70	1·07	39	1·45	86*
	4·3	2·04	68	1·55	177*
	3·73	1·64	35	1·85	102*
	3·91	1·37	43	2·27	72
	2·98	1·21	61	1·43	108*
	3·02	1·19	53	1·52	99*
				Average—2·06	

APPENDIX A—(continued).

Species.	Weight of insect with full crop (mg.).	Volume of crop contents (mm.³).	Percentage of sugars in crop contents.	Weight of insect empty (mg.).	Load as percentage of empty weight.
Apis :	126	17·2	15	108	17
	167	54·7	22	108	55*
	152	55·6	5	96	58*
	142	41·2	12	99	43*
	133	40·2	15	89	48*
	144	26·1	27	115	25
	119	28·3	6	90	32
	124	15·8	22	107	16
	132	19·3	32	110	20
	172	42	30	125	38*
	126	18	8	107	17
	134	32	16	100	34
	124	21	12	102	22
	135	27	34	104	30
	118	19	16	98	21
	188	79	26	101	86*
	171	59	5	111	54*
	160	39·5	25	117	37*
	169	54	28	108	56*
	136	38	15	96	42*
			Average—	105	
Drosophila :	0·91	0·00	24	0·910	0
	1·02	0·086		0·925	10
	0·94	0·072		0·861	9
	0·87	0·091		0·770	13*
	0·93	0·108		0·811	15*
	0·89	0·068	24	0·815	9
	1·05	0·160		0·874	20*
	1·10	0·180		0·902	22*
	1·10	0·180	24	0·902	22*
	1·02	0·199		0·801	26*
	1·25	0·280		0·970	39*
			Average—	0·866	

* Apparently fully fed specimens.

Appendix B.

Nectar secretion in Northern Canada.

Species.	Abundance.		Date.	Number of readings.	Range of concentration (per cent. sugars).	Mean sugars per 24 hrs. per flower unit (mg.).	Productivity (mg./acre/day).
Helobiae, Juncaceae :							
Triglochin maritima L.	l.a.		14.vii.51	.	.	*nil*	.
Liliiflorae, Liliaceae :							
Tolfieldia pusilla (Michx.) Pers.	a.		8.vii.51	.	.	*traces*	.
Microspermae, Orchidaceae :							
Cypripedium passerinum Richards	o.		16.vii.51	.	.	*nil*	.
Habenaria hyperborea (L.) R. Br.	l.f.		8.vii.51	2	10	0·11	6
			14.vii.51	.	.	*traces*	.
			24.vii.51	4	*c.*15	0·16	10
			31.vii.51	.	.	*nil*	.
H. obtusata (Pursh.) Richards	f.		1.vii.51	.	.	*traces*	.
			8.vii.51	2	10	0·10	8
			10.vii.51	.	.	*traces*	.
			12.vii.51	4	10–12	0·04	3
			13.vii.51	3	12–19	0·08	6
Orchis rotundifolia Banks	l.f.		13.vii.51	.	.	*traces*	.
Spiranthes Romanzoffiana Cham.	o.		31.vii.51	3	37–47	0·45	3
			5.viii.51	.	.	*nil*	.
Salicales, Salicaceae :							
Salix arctophila Cockerell	l.a.	♂	18.vi.51	4	45–55	2·6	8320
			6.vi.52	11	24–65	2·7	8620
		♀	18.vi.51	5	22–34	1·9	6080
			22.vi.51	6	25–45	2·2	7040
S. cordifolia Hook	l.a.	♂	29.vi.51	2	16–20	1·95	234
			13.vi.51	5	37–40·5	13·5	1620
			7.vi.52	7	12–31	1·6	192
		♀	29.vi.51	3	14–19	1·1	132
			5.vi.52	3	46–50	1·75	210
			7.vi.52	4	16–25	1·33	162
S. planifolia Pursh	l.a.	♂	12.vi.51	3	32–34	2·7	6480
		♀	13.vi.51	3	45–48	1·2	2880
S. candida Flügge	l.f.	♂	3.vi.52	4	9–21	1·9	204
		♀	5.vi.52	3	8–18	c.0.9	96
S. reticulata L.	a.	♂	6.vi.52	1	73	.	.
			7.vi.52	3	7–9	0·22	352
		♀	6.vi.52	1	70	.	.
			7.vi.52	3	14–18	0·05	80
S. Richardsonii Hooker	l.f.	♂	11.vi.52	3	26–30	2·60	188
		♀	11.vi.52	3	16–23	1·70	124
Myricales, Myricaceae:							
Myrica gale L.	l.f.		17.vi.51	.	.	*nil*	.

APPENDIX B—(continued).

Species.	Abundance.	Date.	Number of readings.	Range of concentration (per cent. sugars).	Mean sugars per 24 hrs. per flower unit (mg.).	Productivity (mg./acre/day).
POLYGONALES, Polygonaceae :						
Polygonum viviparum L.	l.f.	16.vii.51	3	17–20	0·15	4
Rumex fenestratus Greene	o.	19.vii.51	.	.	*nil*	.
		20.vii.51	.	.	,,	.
CARYOPHYLLALES, Caryophyllaceae :						
Arenaria lateriflora (L.) Feugh	o.	13.vii.51	1	20	0·11	.
		14.vii.51	3	17–23	0·22	1
Cerastium alpinum L.	f.	17.vi.51	.	.	*nil*	.
Stellaria longipes Goldie	l.f.	31.vii.51	1	74	0·82	19
		13.vii.51	.	.	*nil*	.
RANALES, Ranunculaceae :						
Anemone Richardsonii Hook	o.	11.vii.51	.	.	*nil*	.
Caltha palustris L.	l.f.	23.vi.51	4	36–42	0·47	17
Ranunculus lapponicus L.	.	30.vi.51	.	c.70	*traces*	.
R. Purshii Richards	.	8.vii.51	3	38–44	0·19	15
RHOEDALES, Cruciferae :						
Barbarea vulgaris R. Br.	l.f.	28.vi.51	3	32–35	0·19	17
		13.vii.51	.	.	*nil*	.
		14.vii.51	.	.	,,	.
Cardamine pratensis L.	o.	14.vii.51	.	.	,,	.
		20.vii.51	6	14–19	0·32	26
Draba glabella (Pursh)	l.f.	16.vi.51	.	.	*traces*	.
		21.vi.51	.	.	,,	.
Lesquerella arctica (Wormsk) Watson	l.f.	16.vi.51	.	.	,,	.
		21.vi.51	.	.	,,	.
		22.vi.51	.	.	,,	.
ROSALES, Saxifragaceae :						
Parnassia palustris L. var. *neogaea* Fern.	l.f.	17.vii.51	1	10	0·12	5
		20.vii.51	.	.	*nil*	.
		25.vii.51	5	37–52	1·1	44
		14.vii.52	6	72–75	0·22	9
Ribes hudsonianum Richards	o.	9.vii.51	.	.	*traces*	.
R. oxyacanthoides L.	l.f.	7.vi.52	6	12–24	0·72	130
		13.vi.52	7	33–72	1·6	288
R. triste Pall.	o.	23.vi.51	.	.	*traces*	.
Saxifraga Hirculus L.	l.f.	27.vii.51	.	.	*nil*	.
		29.vii.51	1	24	0·26	4
S. oppositifolia L.	l.f.	6.vi.51	6	59	0·76	4
S. tricuspidata Rottb.	f.	6.vi.52	2	48–50	0·55	25
		3.vii.51	1	30	*traces*	.
		11.vii.51	6	23–25	0·41	42
		13.vii.51	4	22–29	0·36	36
		2.vii.51	.	.	*nil*	.

APPENDIX B—(continued).

Species.	Abundance.	Date.	Number of readings.	Range of concentration (per cent. sugars).	Mean sugars per 24 hrs. per flower unit (mg.).	Productivity (mg./acre/day).
Rosaceae :						
Dryas integrifolia Vahl.	l.d.	29.vi.51	2	28–29	0·65	1625
		28.vi.51	3	28–29	0·47	1175
		11.vii.51	3	11–20	0·6	1500
		13.vii.51	4	25–32	0·67	1675
		28.vi.52	6	13–24	0·71	1775
Potentilla Egedei Wormsk.	l.f.	8.vii.51	.	.	*traces*	.
		9.vii.51	6	24–48	0·69	21
P. nivea L.	f.	3.vii.51	.	36	*traces*	.
		13.vii.51	2	18–21	0·16	6
P. palustris (L.) Scop.	f.	25.vii.51	2	13–16	1·4	56
		27.vii.51	6	9–14	4·5	180
Rosa acicularis Lindl.		25.vii.51	.	.	*nil*	.
		1.viii.51	.	.	,,	.
Rubus acaulis Michx.	l.f.	25.vi.51	2	14–20	0·34	12
		29.vi.51	6	68–74	2·3	83
		28.vi.51	2	33–35	0·78	28
		30.vi.51	3	65–72	2·0	72
		8.vii.51	1	38	3·5	126
		10.vii.51	1	27	1·0	36
		12.vii.51	3	12–15	0·59	21
		13.vii.51	2	15–17	0·68	25
R. Chamaemorus L.	f.	22.vi.51	3	43–48	0·38	19
		23.vi.51	5	20–36	0·45	23
		17.vi.51	.	.	*nil*	.
		7.vi.52	2	6–7	0·21	10
		13.vi.52	.	.	*nil*	.
Leguminosae :						
Hedysarum Mackenzii Richardson	l.f.	9.vii.51	3	25–31	0·66	54
		13.vii.51	1	26	0·2	16
		2.viii.51	6	17–29	0·6	48
Oxytropis campestris (L.) D.C.	l.a.	9.vii.51	8	28–42	0·62	750
		31.vii.51	6	31–38	0·66	795
Trifolium hybridum L.		*5.viii.50	3	38–52	.	.
		†10.viii.51	.	.	*nil*	.
T. pratense L.		†10.viii.51	1	28	0·27	
SAPINDALES, Empetraceae :						
Empetrum nigrum L.		14.vi.51	.	.	*nil*	.
MYRTIFLORAE, Onagraceae :						
Epilobium angustifolium L.	l.a.	*5.vii.50	3	54–65	.	.
		15.vii.51	6	42–65	1·8	2170
		21.vii.51	6	24–31	1·5	1800
		22.vii.51	6	70–77	2·4	2880
		24.vii.51	12	24–49	1·6	1920
		2.viii.51	6	29–47	0·88	1056
		†10.viii.51	1	75	1·1	1320

APPENDIX B—(continued).

Species.	Abundance.	Date.	Number of readings.	Range of concentration (per cent. sugars).	Mean sugars per 24 hrs. per flower unit (mg.).	Productivity (mg./acre/day).
E. latifolium L.	l.f.	8.vii.51	6	26–40	3·5	70
		21.vii.51	2	25–28	1·4	28
Oenothera sp.	.	†10.viii.51	1	16	0·37	.
Haloragaceae :						
Myriophyllum exalbescens Fern.	l.f.	27.vii.51	2	33–36	0·12	3
UMBELLIFLORAE, Araliaceae :						
Aralia hispida Vent.	.	*5.viii.50	.	.	*nil*	.
Umbelliferae :						
Cicuta Mackenzieana Raup.	l.f.	29.vii.51	.	.	*traces*	.
		4.viii.51	.	.	,,	.
		5.viii.51	.	.	,,	.
Heracleum maximum Bartr.	o.	17.vii.51	.	.	*nil*	.
ERICALES, Pyrolaceae :						
Moneses uniflora (L.) Gray	l.f.	14.vii.51	.	.	*nil*	.
		18.vii.51	.	.	,,	.
Pyrola grandiflora Radius.	l.a.	25.vii.51	.	.	,,	.
		11.vii.51	.	.	,,	.
		13.vii.51	.	.	,,	.
		16.vii.51	.	.	,,	.
P. minor L.	o.	25.vii.51	.	.	,,	.
P. secunda L.	o.	16.vii.51	5	26–30	0·59	1
		18.vii.51	6	7–15	0·29	.
Ericaceae :						
Andromeda Polifolia L.	l.f.	28.vi.51	6	18–23	0·08	4
		11.vi.52	5	26–38	0·06	3
Arctostaphylos rubra (Rehder and Wilson) Fern.	l.f.	13.vi.51	3	32–36	0·91	728
		7.vi.52	1	30	0·29	232
		12.vi.52	4	16–22	0·31	248
Kalmia angustifolia L.	.	*5.viii.50	.	.	*nil*	.
K. polifolia Wang.	o.	18.vi.51	.	.	*traces*	.
Ledum groenlandicum Oeder	a.	8.vii.51	6	20–28	0·58	4600
		19.vii.51	3	16–25	0·34	2720
		26.vi.52	8	66–77	0·41	3290
		29.vi.52	4	51–55	0·38	3040
L. palustre L. var. *decumbens* Ait.	l.a.	30.vi.51	3	43–56	0·31	1990
		25.vi.51	.	.	*nil*	.
		28.vi.51	.	.	,,	.
		21.vi.52	8	38–54	0·14	900
		29.vi.52	4	51–55	0·17	770

APPENDIX B—(continued).

Species.	Abundance.	Date.	Number of readings.	Range of concentration (per cent. sugars).	Mean sugars per 24 hrs. per flower unit (mg.).	Productivity (mg./acre/day).
Rhododendron lapponicum (L.) Wahlenb.	a.	10.vii.48	1	89	.	.
		18.vi.51	2	15–21 (rain)	.	.
		22.vi.51	7	68–76	2·7	16200
		11.vii.51	3	42–48	0·65	3900
		28.vi.52	6	62–76	1·08	6480
		6.vi.52	10	35–46	0·47	2820
Vaccinium oxycoccus L.	l.a.	10.vii.51	4	28–33	.	.
		12.vii.51	.	high	*traces*	.
V. uliginosum L.	l.a.	28.vi.51	3	8–13	0·26	624
		16.vii.51	1	24	0·31	744
V. Vitis-Idaea var. *minus* Lodd.	l.f.	26.vi.52	.	.	*traces*	.
PRIMULALES, Primulaceae :						
Androsace septentrionalis L.	l.a.	17.vi.51	.	.	*nil*	.
Primula egaliksensis Wormsk.	l.f.	16.vi.51	.	.	*traces*	.
		28.vi.51	4	21–25	0·36	28
Primula stricta Hornem.	o.	14.vii.51	.	.	*nil*	.
CONTORTAE, Gentianaceae :						
Menyanthes trifoliata L.	l.f.	20.vii.51	1	11	0·1	.
TUBUFLORAE, Convolvulaceae :						
Convolvulus sepium L.		†10.viii.51	.	.	*nil*	.
Boraginaceae :						
Mertensia maritima (L.) S.F. var. *tenella* Fries	o.	16.vii.51	2	32	0·47	23
Labiatae :						
Scutellaria epilobiifolia A. Hamilt.		*5.viii.50	3	58–69	.	.
Scrophulariaceae :						
Castilleja Raupii Pennell	l.a.	28.vi.51	.	.	*traces*	.
		1.vii.51	3	33–36	0·39	218
		8.vii.51	4	25	0·55	308
		13.vii.51	4	29–32	0·68	370
		19.vii.51	2	22–29	0·25	140
		1.viii.51	5	26–33	0·41	230
		2.viii.51	1	76	0·85	475
Pedicularis flammea L.	l.f.	25.vi.52	.	.	*traces*	.
P. labradorica L.	.	27.vi.52	.	.	,,	.
P. lapponica L.	l.f.	29.vi.51	3	28–31	0·34	7
P. sudetica Willd.	o.	11.vii.51	.	.	*nil*	.
		25.vi.52	.	.	*traces*	.

APPENDIX B—(continued).

Species.	Abundance.	Date.	Number of readings.	Range of concentration (per cent. sugars).	Mean sugars per 24 hrs. per flowers unit (mg.).	Productivity (mg./acre/day).
Lentibulariaceae :						
Pinguicula villosa L.	o.	20.vii.51	.	.	*nil*	.
P. vulgaris L.	f.	24.vii.51	1	c.6	0·06	1
		31.vii.51	.	.	*traces*	.
CAMPANULATAE, Campanulaceae :						
Campanula rotundifolia L.	.	†10.viii.51	.	.	*nil*	.
Compositae :						
Achillea Millefolium L.	f.	10.vii.51	1	31	0·11	22
		13.vii.51	3	26–29	0·12	24
		*5.viii.50	.	.	*nil*	.
		1.viii.51	.	.	,,	.
		2.viii.51	.	.	,,	.
		4.viii.51	.	.	,,	.
Anaphalis margaritacea (L.) C. B. Clarke	.	*5.viii.50	.	.	,,	.
Arnica attenuata Greene	l.a.	13.vii.51	4	32–41	0·32	102
		2.viii.51	1	29	1·1	352
		5.vii.52	4	17–24	0·68	218
Aster sp.	.	*5.viii.50	.	.	*nil*	.
Erigeron elatus (Hooker) Greene	l.f.	19.vii.51	.	.	,,	.
Matricaria inodora L. var. *nana* (Hooker) T. & G.	l.f.	11.vii.51	.	.	,,	.
		2.viii.51	.	.	,,	.
Petasites sagittatus (Pursh) Gray	f.	16.vi.51	.	.	*traces*	.
		5.vi.52	24	.	,,	.
Senecio congestus (R. Br.) D. C.	l.a.	20.vii.51	2	12	0·28	202
		1.viii.51	4	25–35	0·46	332
		5.vii.52	4	24–29	0·58	419
Solidago multiradiata Ait.	l.f.	29.vii.51	.	.	*traces*	.
Solidago sp.	.	*5.viii.51	.	.	*nil*	.
		†10.viii.51	.	.	,,	.
Taraxacum russeolum Dahlstedt	l.f.	9.vii.51	3	33–42	2·7	11

* Goose Bay, Labrador.
† Mafeking, Manitoba.
All other readings at Churchill, Man.

d = dominant.
a = abundant.
f = frequent.
o = occasional.
r = rare.
l = locally.

APPENDIX C.

Speeds of flight and distances flown on measured amounts of glucose.

Specimen and test number.	Final weight (mg.).	Sugar fed (mg.).	Flight time (sec.).	Distance (max. non-stop) (m.).	Mean speed (max.) (cm./sec.).	Sugar consumption (mg./hour).
Tabanus affinis : 1/1 to 2/1 on threads, 2/2 to 7/3 on large straw mill, remainder on 2 metre mills, *with small baffle, **with large baffle.						
1/1	.	2·75	975	.	.	10·2
1/2	.	2·48	845	.	.	10·6
1/3	.	0·44	145	.	.	10·92
1/4	.	2·94	1351	.	.	7·83
2/1	.	2·04	1248	.	.	5·9
2/2	.	2·67	3136	4938 (2950)	157 (175)	3·07
3/1	.	2·75	1993	3698 (2967)	186 (202)	4·97
4/0	.	.	10983	28350 (27720)	258 (608)	.
4/1	.	5·06	3500	8346 (7245)	238 (475)	5·20
4/2	.	5·50	4351	9930 (9400)	228 (454)	4·6
5/1	.	1·375	566	1980 (1743)	350 (458)	8·75
5/2	.	1·375	734	2214 (1604)	302 (333)	6·74
6/1	.	5·50	1662	5770 (4398)	348 (492)	11·99
6/2	.	5·50	1960	6310 (5620)	324 (558)	10.1
7/1	.	6·15	3680	9800 (5502)	267 (395)	6·02
7/2	.	2·16	2155	4670 (4193)	217 (370)	3·6
7/3	.	2·16	2233	4748 (3271)	212 (325)	3·5
8/1	125	2·56	1740	4650 (4291)	267 (512)	5·3
8/2	125	2·56	1550	3960 (3562)	255 (410)	6·0
8/3	125	1·72	1510	3398 (3241)	225 (292)	4·1
8/4	125	2·46	2105	3890 (3421)	185 (283)	4·22
8/5	125	4·30	5180	8571 (6802)	165 (392)	2·99
9/1	154	2·56	2305	6413 (6170)	278 (436)	4·0
9/2	154	2·56	2615	5071 (4184)	194 (370)	3·5
10/1	166	5·22	2715	7900 (5730)	291 (412)	6·9
10/2	166	2·56	1260	4048 (3941)	321 (512)	7·3
10/3	166	2·56	2330	5423 (4150)	232 (333)	4·0
10/4	166	2·56	2270	4627 (4053)	204 (530)	4·1
11/1	138	2·91	3205	5613 (5178)	175 (658)	3·27
11/2	138	1·28	1420	2813 (2634)	198 (325)	3·2
11/3	138	2·56	2665	5824 (4970)	218 (333)	3·5
11/4	138	2·56	2990	6012 (2536)	201 (283)	3·1
11/5	138	2·56	3100	6167 (5012)	199 (320)	2·98
11/6	138	2·56	2560	6268 (5481)	245 (436)	3·6
11/7	138	2·56	1875	4552 (4261)	243 (412)	4·92
11/8	138	2·56	2125	4379 (4228)	206 (283)	4·34
11/9	138	6·50	7560	15670 (12080)	207 (300)	3·1
12/1	110	3·92	5835	8071 (6516)	138 (204)	2·4
12/2	110	5·22	6930	9930 (6662)	143 (180)	2·7
12/3	110	5·22	10310	13923 (12750)	135 (177)	1·8
13/0	133	.	3890	11080 (7710)	286 (483)	.
14/0	133	.	2620	4141 (3014)	158 (233)	.
14/1	133	5·22	5805	6510 (5599)	112 (217)	3·2
14/2	133	0·78	700	1638 (1518)	234 (410)	4·01
14/3	133	2·56	2275	3670 (3595)	161 (350)	4·1
*14/4	133	2·56	3170	4060 (2325)	128 (200)	2·9
*14/5	133	2·56	3190	3900 (2460)	122 (125)	2·90
**14/6	133	2·56	2820	3615 (2145)	128 (180)	3·30

APPENDIX C—(continued).

Specimen and test number.	Final weight (mg.).	Sugar fed (mg.).	Flight time (sec.).	Distance (max. non-stop) (m.).	Mean speed (max.) (cm./sec.).	Sugar consumption (mg./hour).
**14/7	133	2·56	3310	4510 (4120)	136 (175)	2·8
14/8	133	2·56	3050	5950 (5290)	195 (334)	3·0
14/9	133	11·20	12610	18669 (12208)	148 (310)	3·2
14/10	133	5·22	3990	9072 (8281)	227 (333)	4·7
14/11	133	3·89	4710	7931 (7250)	168 (367)	3·0
15/1	136	5·22	2520	7571 (7136)	300 (581)	7·5
15/2	136	2·11	1520	3534 (3164)	232 (579)	5·0
15/3	136	2·56	2150	5030 (4251)	234 (512)	4·3
*15/4	136	2·43	1610	4425 (3857)	275 (352)	5·4
*15/5	136	2·56	2070	4830 (4223)	233 (328)	4·5
**15/6	136	2·56	2060	5110 (4867)	248 (402)	4·5
**15/7	136	2·56	2950	6180 (5570)	209 (342)	3·1
15/8	136	2·56	1640	5090 (3524)	310 (468)	5·6
15/9	136	5·22	3460	10110 (9291)	292 (490)	5·4
15/10	136	12·00	4460	14960 (12610)	335 (579)	9·7
15/11	136	2·56	3050	6147 (5603)	201 (420)	3·0
16/0	127	.	3200	5893 (5571)	184 (410)	.
17/1	174	2·56	2490	5531 (5370)	222 (319)	3·7
17/2	174	2·38	1610	3899 (2987)	245 (510)	5·3
17/3	174	2·38	1630	4180 (4025)	257 (483)	5·3
17/4	174	3·85	3080	7598 (7441)	246 (492)	4·5
17/5	174	2·38	1724	3925 (3310)	228 (352)	4·97
17/6	174	2·38	1560	4160 (3642)	267 (434)	5·5
18/1	171	2·38	2430	5318 (3963)	219 (345)	3·5
18/2	171	2·38	1640	4043 (3732)	246 (325)	5·2
18/3	171	2·38	1505	3662 (2608)	243 (367)	5·7
19/0	138	.	1580	5094 (3520)	322 (460)	.
19/1	138	2·38	968	3640 (3018)	375 (533)	8·85
Tabanus septentrionalis : 1/0 to 2/5 on small straw mill, 3 on large straw, 4 on 1·5 m. and 5 on 1·0 m. mills. 2/1 and 3/1 on sucrose.						
1/0	56·5	.	6493	.	.	.
1/1	56·5	2·12	2507	6814 (6213)	272 (275)	3·04
1/2	56·5	1·3	1655	3952 (2728)	238 (265)	2·83
2/1	61·2	1·65	1232	3314 (436)	268 (300)	4·82
2/2	61·2	2·46	1618	4450 (2153)	275 (312)	5·47
2/3	61·2	2·46	1579	4455 (2412)	282 (612)	5·61
2/4	61·2	1·23	1247	3526 (1619)	283 (325)	3·55
2/5	61·2	0·74	898	2277 (1129)	253 (283)	2·97
3/1	56·5	0·74	765	2097 (1656)	274 (440)	3·48
4/0	48·3	.	4600	4956 (1423)	108 (120)	.
5/0	49·2	.	2990	3078 (672)	103 (233)	.
Aëdes nearcticus : 1 and 9 on 0·75 m. mill, 2 on 0·5 m., remainder on 1·0 m. mills.						
4/1	2·5	0·0945	6990	6900 (4045)	100 (106)	0·0486
4/2	2·5	0·144	7055	6850 (1240)	97 (125)	0·0735
5/1	2·4	0·121	9900	7328 (4872)	74 (82)	0·0440
5/2	2·4	0·212	14750	9760 (4274)	66 (85)	0·0517
6/1	3·0	0·125	4710	5645 (5520)	120 (132)	0·0956
6/2	3·0	0·185	6710	7520 (7274)	112 (136)	0·0993

APPENDIX C—(continued).

Specimen and test number.	Final weight (mg.).	Sugar fed (mg.).	Flight time (sec.).	Distance (max. non-stop) (m).	Mean speed (max.) (cm./sec.).	Sugar consumption (mg./hour).
6/3	3·0	0·185	8455	7780 (6180)	92 (112)	0·0788
7/1	2·4	0·077	6810	5106 (1263)	75 (112)	0·0407
8/1	2·1	0·0447	1653	1954 (296)	118 (134)	0·0973
9/1	2·1	0·0297	1665	1982 (1542)	119 (158)	0·0643
Aëdes flavescens : on small straw mill.						
1/0	8·15	.	5234	8340 (7922)	159 (252)	.
1/1	8·15	0·825	10308	10180 (9785)	98 (160)	0·288
1/2	8·15	0·275	4875	3852 (2560)	79 (154)	0·202
Simulium venustum : all on 1·0 m. mill.						
1/1	2·3	0·061	2580	4495 (3970)	174 (185)	0·085
1/2	2·3	0·091	4160	6413 (1431)	154 (185)	0·079
1/3	2·3	0·152	6170	9198 (1775)	149 (185)	0·089
2/1	2·55	0·119	6590	9296 (5260)	141 (168)	0·065
2/2	2·55	0·158	3370	6778 (6486)	201 (238)	0·169
2/3	2·55	0·116	3300	6412 (5810)	194 (223)	0·127
3/0	2·05	.	2090	2047 (698)	98 (119)	.
3/1	2·05	0·0595	4455	5082 (1964)	114 (135)	0·0481
4/1	2·8	0·145	2070	8478 (8060)	167 (206)	0·103
4/2	2·8	0·340	12360	18920 (15840)	153 (194)	0·099
4/3	2·8	0·136	6770	11680 (11450)	173 (225)	0·0723
4/4	2·8	0·215	5490	9882 (2100)	180 (208)	0·141
4/5	2·8	0·175	6120	9930 (6432)	162 (196)	0·103
5/1	2·4	0·042	3050	3450 (2215)	113 (133)	0·0496
6/1	2·4	0·039	2820	3360 (1522)	119 (144)	0·0498
7/1	2·3	0·076	6650	6994 (6410)	105 (176)	0·0411
Simulium vittatum : all on 1·0 m. mill.						
1/1	1·95	0·077	2290	4532 (3970)	198 (270)	0·121
1/2	1·95	0·11	2880	7814 (7120)	271 (293)	0·138
1/3	1·95	0·0865	2440	6470 (2924)	265 (295)	0·128
Apis mellifera : all on 1·0 m. mill.						
1/1	89	2·45	2202	4338 (4081)	197 (332)	4·0
1/2	89	1·375	480	1344 (1153)	280 (372)	10·3
1/3	89	2·75	988	3478 (2201)	352 (418)	10·0
2/1	80	2·75	1762	4581 (1168)	260 (382)	5·6
2/2	80	2·75	1318	3453 (3230)	262 (372)	7·51
2/3	80	2·75	1525	3569 (1300)	234 (372)	6·5
2/4	80	2·75	1540	3357 (1134)	218 (382)	6·45
2/5	80	2·75	1570	4270 (1548)	272 (382)	6·3
3/1	84	2·75	2550	5253 (4739)	206 (260)	3·88
3/2	84	2·75	1968	5700 (1762)	188 (250)	5·03
4/1	80	2·75	991	2587 (2435)	261 (358)	10·0
4/2	80	2·75	942	2449 (2387)	260 (318)	10·5
4/3	80	2·75	1038	2896 (2743)	279 (360)	9·5
5/1	83	2·2	891	2031 (1948)	228 (298)	8·9
6/1	85	2·75	1150	3780 (3680)	329 (410)	8·6
7/1	83	2·75	1302	4024 (3973)	308 (391)	7·6

APPENDIX C—(continued).

Specimen and test number.	Final weight (mg.).	Sugar fed (mg.).	Flight time (sec.).	Distance (max. non-stop) (m.).	Mean speed (max.) (cm./sec.).	Sugar consumption (mg./hour).
***Drosophila* :** all on 0·5 m. mill.						
1/1	0·65	0·065	6720	10406 (2906)	155 (165)	0·0348
2/1	0·72	0·0089	2124	2737 (1110)	129 (142)	0·0151
2/2	0·72	0·0167	3215	4110 (694)	128 (137)	0·0186
3/1	0·61	0·019	2940	4090 (3340)	139 (154)	0·0233
3/2	0·61	0·0223	3362	5034 (3310)	150 (156)	0·0240
3/3	0·61	0·0179	2365	3553 (1802)	150 (170)	0·0272
3/4	0·61	0·029	3520	5380 (1230)	153 (165)	0·0297
4/1	0·68	0·0257	4090	5810 (5010)	142 (163)	0·0227
4/2	0·68	0·0268	4220	6180 (4925)	146 (165)	0·0229
5/1	0·86	0·0098	1760	2395 (445)	136 (142)	0·0204
5/2	0·86	0·0201	2430	3381 (1083)	139 (150)	0·0297
6/1	0·56	0·0173	2600	3790 (1435)	146 (159)	0·0239
7/0	0·78	.	9605	15350 (7434)	160 (168)	.
7/1	0·78	0·0082	1515	2015 (1226)	133 (159)	0·0195
7/2	0·78	0·0105	1843	2307 (591)	125 (131)	0·0196
8/1	0·70	0·009	1905	2482 (2082)	130 (141)	0·0170
8/2	0·70	0·0115	2180	2974 (1692)	136 (151)	0·0190
8/3	0·70	0·0055	990	1356 (437)	137 (146)	0·0200
9/0	.	.	7140	11200 (2745)	157 (181)	.
9/1	.	0·0166	2600	3720 (2347)	143 (157)	0·0230
10/0	0·67	.	8180	14550 (5074)	178 (180)	.
10/1	0·67	0·0156	2504	3535 (851)	141 (143)	0·0224

APPENDIX D.

Conversion factors, constants and symbols.

Conversion Factors.

1 km. = 0·62 mile.
1 inch = 2·54 cm.
1 mile = 1·61 km.
1 lb. = 454 gm.
100 cm./sec. = 2·24 m.p.h.
1 horse-power = 746 watts = 178 cal./sec. = $7{\cdot}46 \times 10^9$ erg/sec.
$1{\cdot}64 \times 10^7$ erg/gm./sec. = 1 h.p./lb.
1 mg. glucose/hr. = 3·74 cal./hour = $1{\cdot}56 \times 10^8$ erg/hr.
= $4{\cdot}335 \times 10^4$ erg/sec.
= 0·7462 c.c. O_2/hr.

Constants.

1 gm. glycogen requires 829·3 c.c. O_2 for oxidation and gives 4·20 cals.
1 gm. glucose requires 726·2 c.c. O_2 for oxidation and gives 3·74 cals.
1 gm. animal fat requires 2013·2 c.c. O_2 for oxidation and gives 9·50 cals.
(*from* Carpenter, 1939.)
1 cal./sec. = 4·183 watts = $4{\cdot}183 \times 10^7$ erg/sec.
Density of air at 760 mm. and 60° F. 0·00122 gm./c.c.
g = 981 cm./sec.^{2}

Symbols.

M = Mass of insect.
T = Thrust generated by wing action.
L = Total lift = vertical component of T + lift from airfoil action of body surfaces.
L_a = Lift from airfoil action of body surfaces.
L = The linear dimensions of insects.
d_p = Parasite or minimum drag on insect without wings.
d_i = Induced drag, or drag increment due to the inclination of the body.
CD = The drag coefficient.
E = The maximum total energy carried.
m = The mass of air passing through the vibrating wings per second.
A = The area of the wings of one side.
θ = The true maximum amplitude of wing beat in radians.
n = The mean frequency of wing beat.
S = The maximum area of the transverse section of the mesothorax.
e_o = The overall efficiency.
R = The range of flight.
t = The duration of flight.
V = The air speed.
l = The wing length.
k = The wing action constant.
ρ = Density of the air.

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PLATE I.

Fig. 1.—*Aëdes punctor* with a pollinium of *Habenaria obtusata* attached below the right eye.

Fig. 2.—The swarming sites of female *Aëdes punctor*. (See Table V.)

Fig. 3.—*Salix arctophila*, female, an important nectar-bearing plant on the tundra. (See Table VII.)

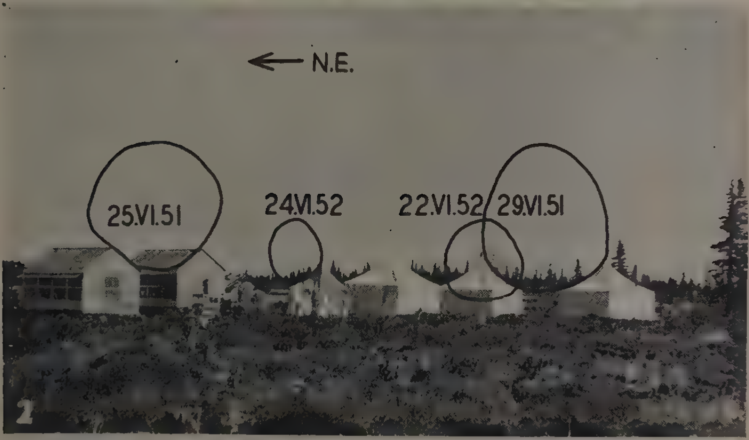
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PLATE II.

IMPORTANT SOURCES OF NECTAR ON THE TUNDRA.

FIG. 1.—*Rhododendron lapponicum.*

FIG. 2.—*Dryas integrifolia.*

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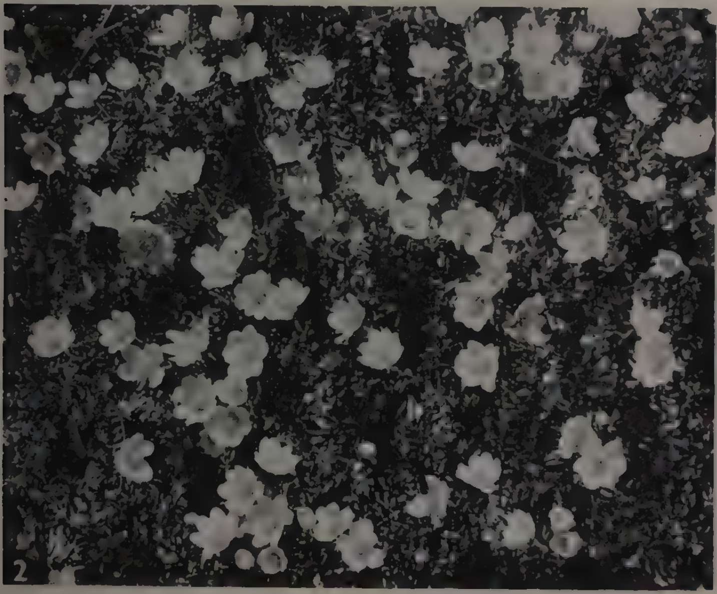

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PLATE III.

Important Nectar-bearing Plants in the Forest.

Fig. 1.—*Ledum palustre.*

Fig. 2.—*Epilobium angustifolium.*

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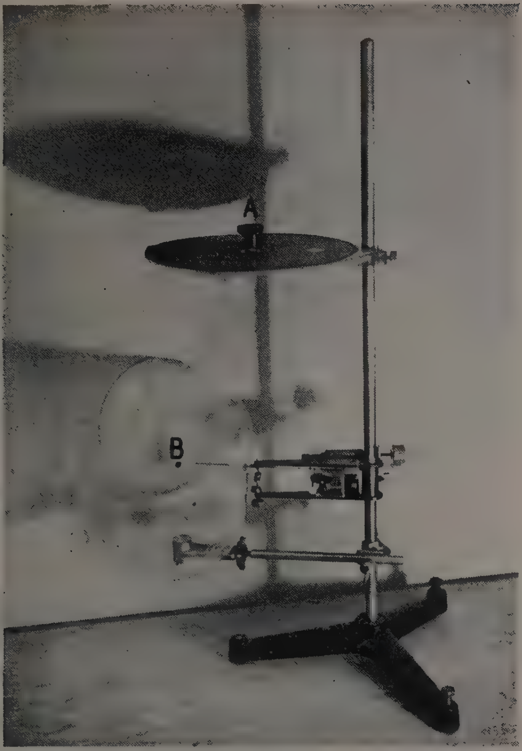
PLATE IV.

The aerodynamic balance in the working section of the wind tunnel. A, Torsion head. B, Insect mounted on needle. C, Chain balance. D, Chain balance control and scale. E, Cradle on which needle is pivoted. F, Viewing mirror. G, Oil damping chamber. H, Plumb bob.



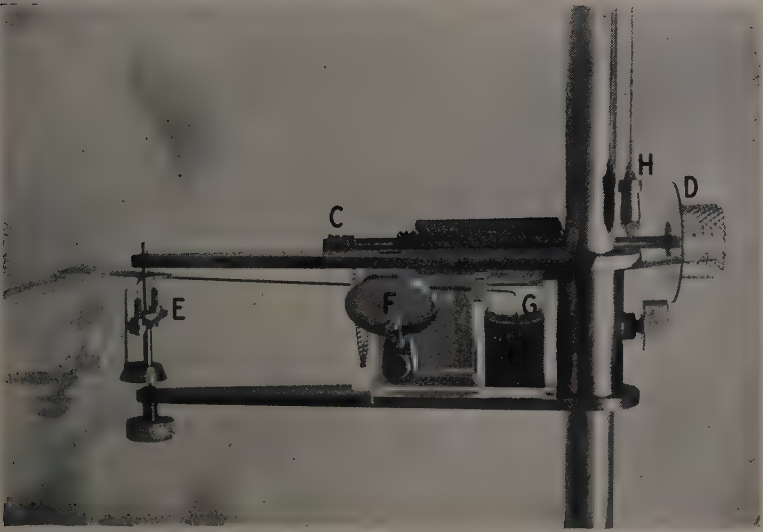


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PLATE V.

FIG. 1.—The holder used for mounting insects for the flight mills. A, Lucite base. B, Vulcanite blocks. C, Lucite wing clamps. D, Rubber bands.

FIG. 2.—The arrangement of the flight mill, amplifier and kymograph. The arm supporting the second mill (not shown) was arranged at right angles. A, Landing "mushroom." B, Photocell. C, Amplifier. D, Time marker and stylus. E, Electrosensitive paper on spiralling kymograph drum.

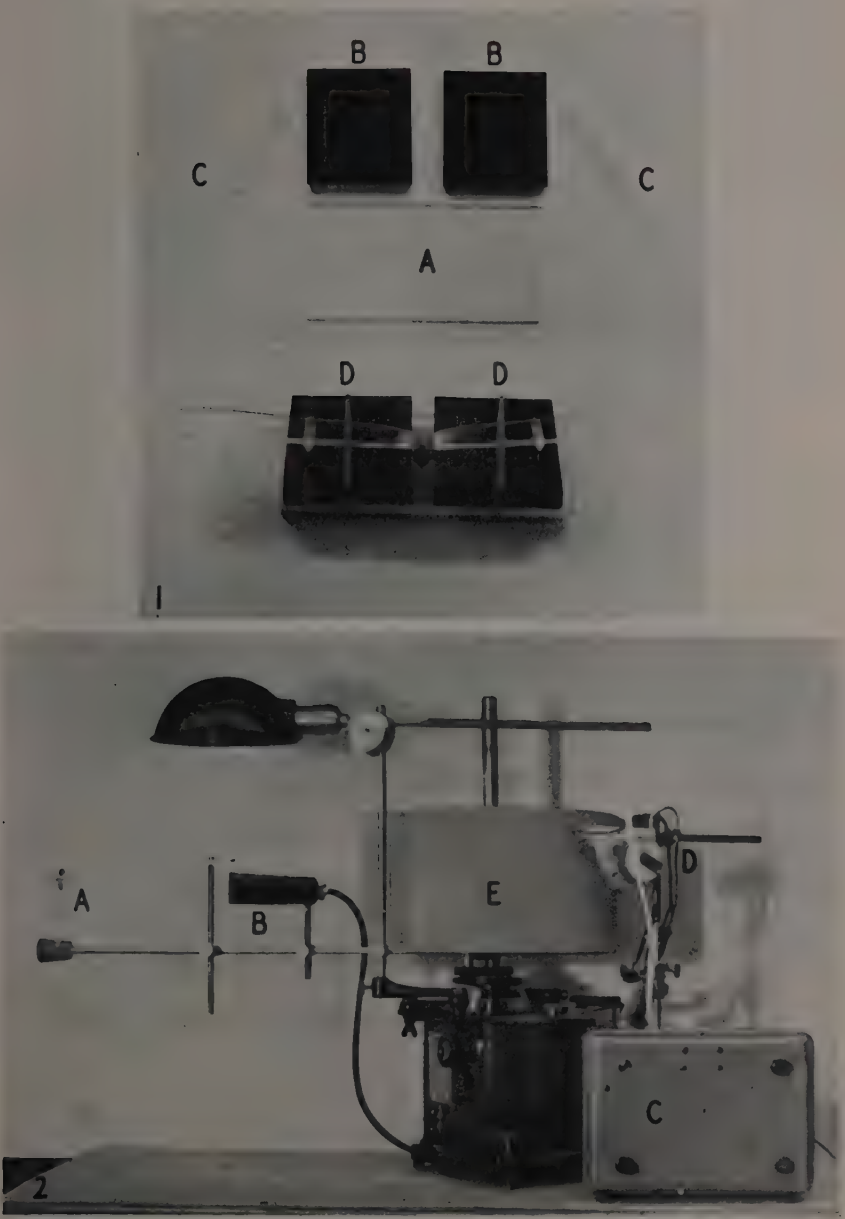
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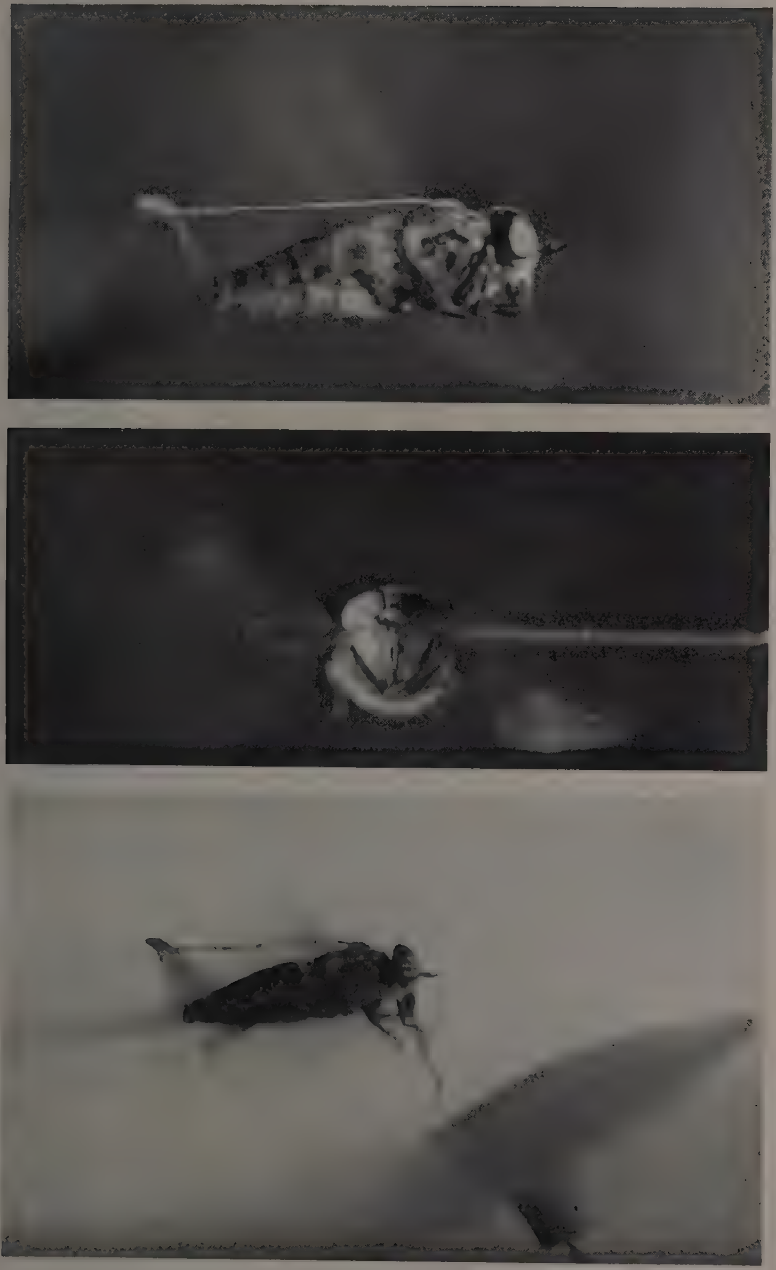
PLATE VI.

The attitude of *T. affinis* in full flight, and the grappling reaction when about to land on the landing "mushroom."



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A REVISION OF THE GENUS *HYPTIOGASTER* KIEFFER (HYMENOPTERA : GASTERUPTIONIDAE), WITH DESCRIPTIONS OF TWO NEW GENERA AND THREE NEW SPECIES.

By R. W. Crosskey, B.Sc., F.R.E.S.

Manuscript received 5th December, 1952.
(Read 6th May, 1953.)

With 25 Text-figures.

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Introduction.

This paper is intended as a monographic revision of those forms of Gasteruptionidae (Hymenoptera) which are characterised by the possession in the fore wing of two closed discoidal cells (1M and Cu_1) *and* the cubitus (Rs + M + M) arising from the basal vein (in part Rs, in part M) as shown in fig. 1. In this type of wing therefore the basal border of the 1st discoidal cell is formed from a free part of M, whereas in all other Gasteruptionidae M is fused in part with Cu_1 and in part with Rs in the middle region of the wing ; in both cases M is a free vein apically. This venational nomenclature is that previously adapted by the author (1951) from Ross.

The last monograph of these forms was that of Kieffer in *Das Tierreich* (1912); a number of "species" in that work are undoubtedly synonyms, and the generic segregations employed are neither, in the present author's view, natural or particularly convenient; further, a number of additional species have been described since 1912, so that it was felt that the group as a whole was in need of revision. As a result of this revision two new genera have been proposed and two of Kieffer's very small genera suppressed, while three additional species of *Hyptiogaster* have been described as new.

The insects concerned here are from the Australasian Region (Australia, Fiji Islands, and the New Hebrides, but not New Zealand), and from the Neotropical Region (Brazil and Argentina).

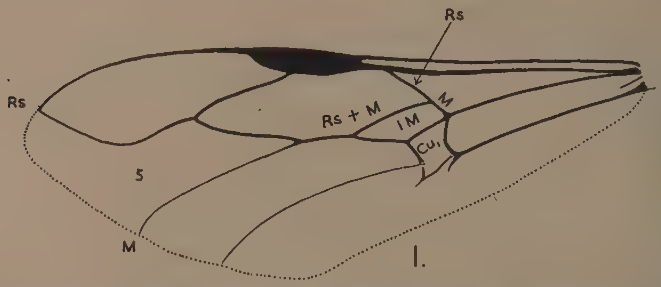


Fig. 1.—*Carinafoenus rufus* Westwood, fore wing showing the venation in Hyptiogastrinae. 1 M, 1st discoidal cell; Cu$_1$, second discoidal cell; Rs + M, cubitus; vein labelled Rs, together with vein labelled M, basal vein.

1. Historical Survey.

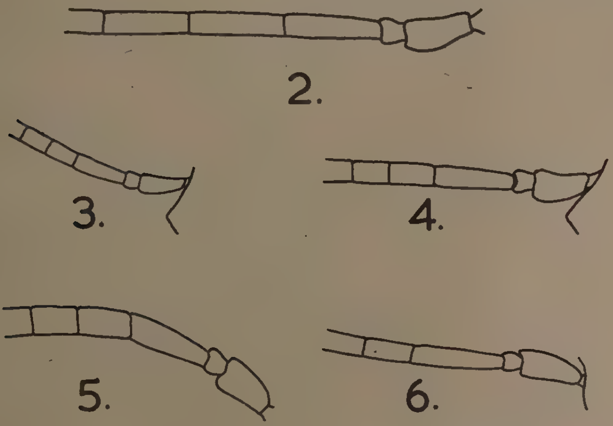
The genus *Hyptiogaster* was erected by Kieffer (1903) to include those species previously assigned to *Gasteruption* Latreille which possess the two discoidal cells and the cubitus springing from the basal vein. At this time it was held to contain ten species, viz. *Gasteruption crassiceps*, *G. antennale*, *G. macronyx*, *G. fallax*, *G. plicatum*, *G. humerale* and *G. infumatum* of Schletterer (1889), and *G. darwinii*, *G. rufum* and *G. australe* of Westwood (1835 and 1841). Schletterer (1893) later described *G. deletangi* from Argentina; the year after publishing his genus *Hyptiogaster*, Kieffer noticed that *G. deletangi* Schletterer should be included under that generic name, and published (1904, *Bull. Soc. Metz* **23**) the new combination, together with the description of another new species from the Neotropical Region, *H. szépligetii*.

The next addition to *Hyptiogaster* came three years later, when Kieffer (1907) described two more Australian species, *H. crassitarsis* and *H. flavinervis*. A further three years elapsed, when Kieffer (1910) removed *H. humeralis* (Schletterer) from *Hyptiogaster* and on the grounds of its toothed pronotum created for it a new genus, *Odontofoenus*.

Odontofeonus remained monotypic until the following year, when Kieffer (1911) described a second species with the toothed pronotum, *O. flavosignatus*; he also described four new species of *Hyptiogaster*, viz., *H. grossitarsis*, *H. macrochela*, *H. pilosa* and *H. microchela*. In the same paper the nomenclature then became rather confused because he removed his species described in 1904 as *H. szépligetii* and erected for it the monotypic genus *Aulacofoenus* ; in addition he described another genus *Hemifoenus* to accommodate a single species *H. brevithorax*, which was unusual in its subquadrate thorax and in its asymmetrical hind tarsi, although the latter character was omitted from the generic diagnosis.

At this time, 1911, therefore, Kieffer's classification comprised : *Hyptiogaster*, 16 species ; *Odontofoenus*, 2 species ; *Aulacofoenus*, 1 species ; and *Hemifoenus*, 1 species.

A year passed, when Kieffer (1912) published his monograph of Evaniidae in *Das Tierreich* ; *Hemifoenus* remained with one species, and *Aulacofoenus* was extended to include *Foenus crassipes* Smith ; *Hyptiogaster* underwent some alterations, *H. darwinii* (Westwood) being removed to *Pseudofoenus* Kieffer, that genus which was characterised by the possession of only one discoidal cell in the fore wing ; Kieffer suppressed his earlier genus *Odontofoenus* (2 species) as a partial synonym of *Hyptiogaster*, so that after the loss of one species to *Pseudofoenus* and the receipt of two species from *Odontofoenus*, *Hyptiogaster* comprised in all 17 species.



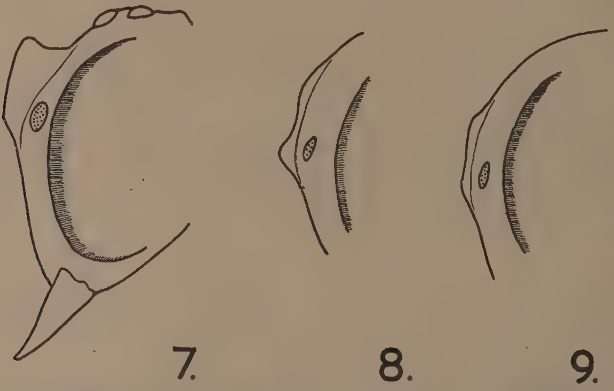
FIGS. 2–6.—Basal segments of the antenna. (2) *Carinafoenus rufus* Westwood ; (3) *Hyptiogaster nitidiuscula* Turner ; (4) *H. inaequalis* Turner ; (5) *Crassifoenus grossitarsis* Kieffer ; (6) *Hyptiogaster patellata* Westwood.

The position remained static until Turner (1918*a*) described six new species of *Hyptiogaster*, viz., *H. arenicola*, *H. asymmetrica*, *H. inaequalis*, *H. nitidiuscula*, *H. floricola* and *H. minima*. Turner rightly re-assigned *darwinii*, which Kieffer had removed to *Pseudofoenus*, to *Hyptiogaster*, and pointed out that *H. macrochela* Kieffer was synonymous with *H. rufa* (Westwood). He also noted that *crassipes* Smith had only one discoidal cell, and that Smith's description was in error in stating that the prescutum extended back to the scutellum (the character on which Kieffer based his *Aulacofoenus*) ; Turner therefore assigned this species to *Pseudofoenus*, which once again reduced *Aulacofoenus* to a monotypic genus.

In the same year Turner (1918*b*) described another new species of *Hyptiogaster* from Fiji, so that as the result of his work the genus now contained 24 species. Brues (1922) removed Turner's Fiji species *H. extranea* from *Hyptiogaster* and assigned it to *Hemifoenus* on the grounds of its subquadrate thorax; but Kieffer's species *Hemifoenus brevithorax* has strongly asymmetrical hind tarsi (fig. 15), while the hind tarsi of *H. extranea* are quite normal and symmetrical; Brues was evidently unaware that the abbreviated thorax is to be found in *H. darwinii* and *H. minima*, and to a lesser extent in other species.

More recently Cheesman (1936) described *Hyptiogaster ritae* from the New Hebrides, and from then on the taxonomy of the group remained stationary until the present revision, except for a catalogue by Hedicke (1939).

The generic name *Eufoenus* was proposed by Szépligeti (1903), concurrently with Kieffer's *Hyptiogaster*, for the Schletterer species *Gasteruption plicatum*, *G. antennale*, *G. humerale* and *G. crassiceps*. *Eufoenus* is synonymous with *Hyptiogaster*; as the names are of the same date Kieffer was in a position to select, being the first reviser, which should stand, and rather forgivably chose his own name, *Hyptiogaster*.



FIGS. 7–9.—Left lateral view of frontal carina. (7) *Hyptiogaster asymmetrica* Turner; (8) *Carinafoenus arenicola* Turner; (9) *Carinafoenus rufus* Westwood.

2. THE PRESENT WORK.

(*a*) Classification adopted and synonymy.

It is considered that the family Gasteruptionidae is divisible into two subfamilies, the Hyptiogastrinae and the Gasteruptioninae; as is so frequently the case with subfamilies these two divisions of the Gasteruptionidae are not particularly easy to characterise, although a student of this group of insects can easily recognise one subfamily from the other on general "facies." An attempt at a strict definition of these two subfamilies is given below:

Fore wing with two closed discoidal cells and the cubitus springing from the basal vein; or with one closed discoidal cell *and* the hind trochanter without a transverse groove. Hind trochanter normally without a transverse groove; if a transverse groove is present, then fore wing with the cubitus arising from the basal vein. Hind femur never with a lobe differentiated off at the base. Ovipositor usually hidden, not protruding beyond the apex of the gaster ; if the ovipositor is long, never longer than the gaster, and the fore wing with the cubitus springing from the basal vein. Sixth sternite of the gaster in the female never divided. Mesonotum very nearly always about as broad as long ; if elongate fore wing with cubitus arising from the basal vein. Hind wing with 3–7 hamuli in an even row. Hind tarsi often sexually dimorphic. Frontal carina sometimes present between the antennae. Form short and thick, head never very prolonged, often about one and a half times or twice as broad as long, thorax deep, sometimes subquadrate, never very elongate, gaster usually short and stout.

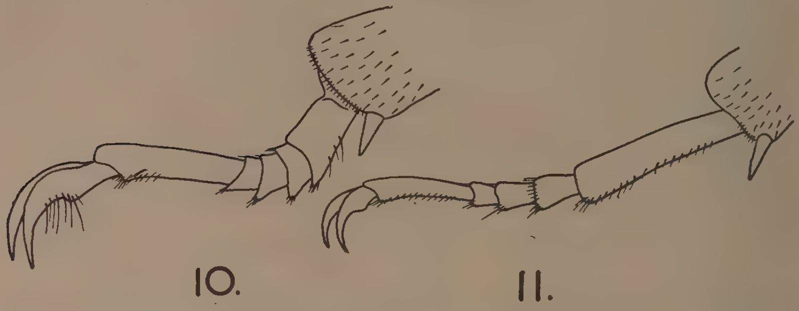
Neotropical, Australasian. Subfamily : **Hyptiogastrinae.**

Fore wing with two closed discoidal cells and the cubitus springing from the end of the median vein ($M + Cu_1$) or from the nervules (cua) ; or with one closed discoidal cell *and* the hind trochanter divided or partially divided into two parts by a transverse groove. Hind trochanter always with a transverse groove. Hind femur with a small lobe differentiated off at the base, sometimes not very distinct. Ovipositor never very short and hidden, always protruding beyond the apex of the gaster, frequently very much longer than the gaster. Sixth sternite of the gaster frequently divided in the female. Mesonotum always elongate. Hind wing with 3 hamuli, usually a more basal singleton and a more apical pair. Hind tarsi not sexually dimorphic. Frontal carina always absent. Form rather long and slender, head often very prolonged behind the eyes, narrow, without well-marked hind angles, thorax elongate, sometimes extremely so, gaster usually very long and slender.

Cosmopolitan, but not New Zealand. Subfamily : **Gasteruptioninae.**

The inclusion in the above definitions of forms with a single discoidal cell involves a consideration of the genus *Pseudofoenus*. It is intended to treat this more fully in a later paper, but from a careful examination of specimens of *Pseudofoenus* the author is of the opinion that the genus is quite artificial and has in fact been derived both from *Hyptiogaster* and from *Gasteruption* (*sensu lato*) ; it is this cleavage of " *Pseudofoenus* " chiefly upon which the division of the family into Hyptiogasterinae and Gasteruptioninae is based. It is evident that some of the species of " *Pseudofoenus* " are nothing but " Hyptiogasters " with a slightly reduced venation, and that the remainder are " Gasteruptions " with a slightly reduced venation—a case, it seems, of convergent evolution. The present revision is therefore a monographic account of Hyptiogastrinae, exclusive of those forms with a single discoidal cell.

In the present work the genus *Hemifoenus* has been suppressed as a partial synonym of *Hyptiogaster*. Kieffer based his genus *Hemifoenus* on the short deep thorax of a single species, but evidently considered the asymmetrical hind tarsi as a supporting character ; but the subquadrate thorax is to be found also in at least three species of *Hyptiogaster*, viz., *darwinii*, *extranea* and *minima*. Since Kieffer's publication of *Hemifoenus* other species of *Hyptiogaster* have been noticed to have asymmetrical hind tarsi, particularly *H. asymmetrica*, *H. darwinii* to some extent, and a new species *H. interrupta*. All *Hyptiogaster* have short thoraces when compared with *Gasteruption*, and in view of the intermediates in degree of asymmetry of the tarsi it is considered that *Hemifoenus* cannot really be regarded as a valid genus. It should be noted, however, that there can be no doubt that the asymmetry of the hind tarsi in *H. asymmetrica* has been derived independently from that in the *H. brevithorax-interrupta-darwinii* complex. Kieffer's small genus *Aulacofoenus* was erected on the strength of a single male (*A. szépligetii*) from Tucuman, Argentina; the British Museum collection contains 7 females which the author believes represent the opposite sex of Kieffer's *Aulacofoenus szépligetii*; but there appear to be no differences sufficiently great to justify segregating them from *Hyptiogaster*, and accordingly the species is included here under the latter genus. It is noteworthy that in his original description of the male Kieffer relegated it to *Hyptiogaster*. These British Museum females have a characteristic anchor-shaped black mark on the mesonotum which agrees with Kieffer's description for the male; the hind tarsi, however, are evidently quite different from Kieffer's male, but this difference is attributed to marked sexual dimorphism which is common in these insects, as for instance in *Carinafoenus flavosignatus* (figs. 10 and 11). According to Kieffer the prescutum in his *Aulacofoenus* extends back to reach the scutellum; it is true that this does not apply to the B.M. females; Kieffer, however, included a species of his own description (*trianguliferum*) in *Gasteruption*, but the type of this has been examined and shows the vein-formation of *Hyptiogaster* (Kieffer's own genus), while his own generic key segregated *Gasteruption* from *Hyptiogaster* on this character. Later he described this species as *Trigonofoenus triangulifer*, although his genus *Trigonofoenus* was defined as possessing the same type of wing-venation as *Gasteruption*. It is concluded that there is sufficient likelihood of the 7 Museum females belonging to *szépligetii* to justify its inclusion in the key and descriptions. *Aulacofoenus*, however, is suppressed as a synonym *pro parte* of *Hyptiogaster*. Two species previously included under *Hyptiogaster* have been removed and are regarded here as constituting a new genus, *Crassifoenus*; the two species concerned, namely *macronyx* and *grossitarsis*, are extremely closely allied, but differ widely from other Hyptiogastrinae in the very large malar area, the incrassate hind legs, the unique form of the hind tarsus (fig. 14) and the equal length of the hind femur and tibia.



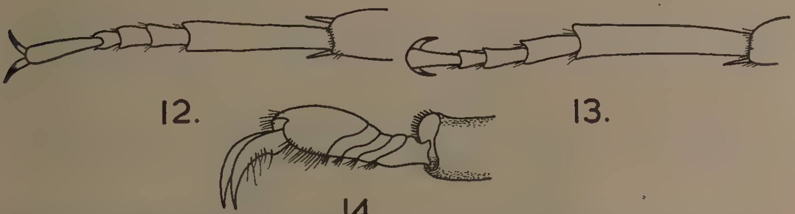
Figs. 10–11.—Hind tarsus of *Carinafoenus flavosignatus* Kieffer; (10) ♀, right lateral; (11) ♂, right lateral.

Five other species previously under *Hyptiogaster*, viz., *crassiceps*, *rufa*, *arenicola*, *flavosignata* and *humeralis*, have been removed to form the genus

Carinafoenus ; these differ from typical *Hyptiogaster* in all possessing a grooved hind trochanter, the fourth antennal segment as long as the third, the long ovipositor, greater number of hamuli, and other characters which will be found under the key to genera and in the generic diagnoses.

The genus *Hyptiogaster* now constituted thus contains 23 species, three of which are described here as new.

The type of Kieffer's *H. microchela* has been examined and the name is considered as synonymous with *Gasteruption patellatum* (Westwood) ; the latter is included here under *Hyptiogaster* for the first time. The types of *Gasteruption trianguliferum* Kieffer (*Trigonogulifer* of Kieffer, 1912) and of *H. australis* (Westwood) have been examined and compared, and Kieffer's name is rejected as a synonym of Westwood's. The types differ slightly in mesonotal sculpture and relative lengths of the basal antennal segments, but these are believed to be differences due to sexual dimorphism only, as Westwood's type is female and Kieffer's male.



Figs. 12–14.—Hind tarsus. (12) *Carinafoenus humeralis* Schletterer, ♂, dorsal ; (13) *C. humeralis*, ♀, dorsal ; (14) *Crassifoenus grossitarsis* Kieffer, inner lateral.

(*b*) Material.

Examination of material has all been carried out at the British Museum (Natural History), which has undoubtedly the largest collection of Hyptiogastrinae. This collection contains at least one specimen of all but 7 species described in this paper, types of 18 species (including two which are suppressed as synonyms), and the cotype of one further species. The numbers of British Museum types are noted in the text of the species descriptions, except in the case of the new species named. The type of another species from the Westwood Collection at Oxford was very kindly loaned to the author, and the loan is acknowledged in section 9. Unfortunately there remained seven species which it proved impossible to see ; three of these are believed to be lodged in the Hofmuseum, Vienna ; as they have not been examined they are excluded from the key to *Hyptiogaster*, but descriptions translated from the originals are given under section 8. The types of the other four species of *Hyptiogaster* are in the Zoologisches Museum der Humboldt-Universität, Berlin. The author communicated with Dr. H. Bischoff, Keeper of the Hymenoptera in that Museum, but was unable to obtain loan of the types, because of customs difficulties in the Soviet sector of Berlin; however, Dr. Bischoff most kindly examined the types on the writer's behalf and reported upon them. It has therefore been possible to incorporate these species in the key and to offer short descriptions of each; it is earnestly hoped that no errors will arise by so doing.

3. SPECIES-GROUPS IN THE GENUS *Hyptiogaster* KIEFFER.

The genus *Hyptiogaster* contains a rather heterogeneous set of diverse species many of which show most unusual, even bizarre, developments, particularly in the character of the frontal carina and of the hind tarsus. It is felt, however, that they must for the present be retained in a single genus, but it is probable that when further species become known, or even when further specimens become available for study, subdivision will be necessary if the group is to bear any semblance of a phylogenetic classification. Some species, e.g., *H. asymmetrica*, are so distinct that they could be segregated into well-definable genera, but the writer is averse to the practice of creating monotypic genera for aberrant off-shoots from the main evolutionary line. Nor is it felt that the erection of a number of subgenera is advisable, as these merely burden the literature with additional names when the same end can be assured by the use of the term "species-group"; the latter term is a particularly happy one as, having no taxonomic significance, it can never lead to over-complicated synonymies or to a belief that an author has created subgenera because he does not dare to make genera.

The species of *Hyptiogaster* fall into at least eight species-groups; these are listed below with an outline of each group's main characteristics:

1. *asymmetrica*-group: frontal carina very strong, like a blunt horn; hind tarsi strongly asymmetrical; hind trochanter with a transverse groove. Only the single very isolated species.
2. *fallax*-group: frontal carina present; hind tarsi symmetrical; hind trochanter with a transverse groove. The single species.
3. *australis*-group: frontal carina present; hind tarsi symmetrical; hind trochanter without a transverse groove; propodeum with a short median carina; terminal flagellar segments elongate. This group contains the most *Gasteruption*-like forms. Three species, *patellata*, *australis*, *ferruginea*. The latter species differs from the other two in the transversely carinate propodeum.
4. *inaequalis*-group: frontal carina present; hind tarsi symmetrical; hind trochanter without a transverse groove; propodeum without a short median longitudinal carina above the hind coxae; terminal flagellar segments subquadrate. Two species, *inaequalis* and *nitidiuscula*. This group, although possessing the frontal carina, shows certain resemblances to the *szépligetii*-group, especially in the hind tarsi.

In all the following groups the frontal carina is absent:

5. *brevithorax*-group: hind tarsi asymmetrical so that all or some segments have a tooth developed on the outer side; mesepimera rectangular, coarsely shagreened, and not reaching the ventral side of the thorax. Three species, *brevithorax*, *interrupta* and *darwini*.

In all the following groups the hind tarsi are symmetrical:

6. *szépligetii*-group : hind trochanter with a transverse groove ; mesonotum red with an anchor-shaped black mark ; the only Neotropical group. Group includes *szépligetii*, *infumata*, and probably *deletangi*.
7. *extranea*-group : prescutum and lateral parts of the scutum strongly raised and with very strong parallel transverse ridges. Only the one species from Fiji. The arched form of mesonotum suggests possible relationship with the *australis*-group.
8. *floricola*-group : the simplest and most typical *Hyptiogaster* ; prescutum not strongly raised and without regular transverse carinae. Contains *pilosa*, *antennalis*, *plicatum*, *microcephala*, *ritae*, *floricola*, and *minima*. The form of the mesepimera in *minima* relate the group to the *brevithorax*-group, *darwini* with its only slightly asymmetrical hind tarsi being a very good intermediate.

4. Key to the Genera of Gasteruptionidae in which the Cubitus arises from the Basal Vein (fig. 1).

1. Malar area large, equal in length to the first antennal segment ; first four segments of the hind tarsus strongly contracted and deeply bilobed, each segment fitting very closely into the preceding one, the fifth segment equal in length to the first four together, thick and strongly convex above with thick pubescence beneath (fig. 14) ; hind femora and tibiae strongly incrassate, the tibia equal in length to the femur Gen. 1. **Crassifoenus** gen. n.

–. Malar area short, much shorter than the first antennal segment, usually about as long as the second ; first four segments of the hind tarsus not strongly contracted and bilobed or close-fitting, the fifth segment almost always much shorter than the four preceding segments together and not markedly convex above ; hind femora not excessively thickened, the hind tibia usually distinctly longer than the femur . 2.

2. Fourth antennal segment about equal in length to the third (fig. 2) ; hind angles of the head well marked, the vertex with at least a trace of a transverse furrow behind the ocelli ; ovipositor long and not hidden ; hind trochanter with a transverse groove ; hind wing with 5–7 hamuli ; hind tarsi always symmetrical but commonly exhibiting sexual dimorphism, those of the female with very enlarged claws ; frontal carina strong . . . . Gen. 2. **Carinafoenus** gen. n.

–. Fourth antennal segment very much shorter than the third (fig. 4) ; head without trace of a transverse furrow ; the hind angles usually not well marked ; ovipositor short, hidden, not protruding beyond the gaster ; hind trochanter almost always without a transverse groove ; hind wing with 3–4 hamuli ; hind tarsi sometimes asymmetrical, normally not sexually dimorphic ; frontal carina commonly absent Gen. 3. **Hyptiogaster** Kieffer

5. Gen. 1. **Crassifoenus** gen. n.

Gasteruptionidae of stout form, the malar area very large, as long as the first antennal segment and longer than the width of the mandible at the base ; head a little wider than the thorax, the hind angles well marked ; strong frontal carina present between the antennal insertions ; third antennal segment much longer than the fourth (fig. 5) ; pronotum without processes, mesonotum almost as broad as long. Hind femora and tibiae strongly incrassate, the tibia about as long as the femur ; first four segments of the hind tarsus very strongly contracted and deeply bilobed, the segments fitting very intimately into one another ; fifth hind tarsal segment about equal in length to the preceding four together, strongly thickened and convex above, with a mat of hair beneath; hind claws very large and as long as the four basal tarsal segments together; the form of the hind tarsi quite unlike any other Gasteruptionidae; hind trochanters with a transverse groove, hind femora without a basal lobe. Fore wings with two closed discoidal cells (1M, Cu_1), and the cubitus (Rs + M + M) springing from the basal vein (anteriorly Rs, posteriorly M) as in fig. 1. Hind wing with 6–7 hamuli. Gaster wrinkled on the dorsum of the first segment; ovipositor very short, hidden, not extending beyond the gaster.

Type-species: *Gasteruption macronyx* Schletterer, 1889, original designation.

2 species, Australia.

(*a*) Key to the species of *Crassifoenus*.

1. Head smooth behind the ocelli; distance between a posterior ocellus and the eye not more than half that between a posterior ocellus and the occipital carina; third antennal segment five times as long as the second; pronotum shagreened, wrinkled in the depressions; wrinkling on the first segment of the gaster reaching to the base
1. **C. macronyx** (Schletterer)

–. Head with a few short longitudinal wrinkles behind the ocelli; distance between a posterior ocellus and the eye three-quarters as great as that between a posterior ocellus and the occipital carina; third antennal segment four times as long as the second; pronotum mainly smooth and shining, rugose-pectinate in the depressions; wrinkling on the first segment of the gaster not reaching right to the base
2. **C. grossitarsis** (Kieffer)

(*b*) Descriptions of the species of *Crassifoenus*.

1. *Crassifoenus macronyx* (Schletterer, 1889).

Gasteruption macronyx Schletterer, 1889, *Ann. naturh.* (*Mus.*) *Hofmus. Wien* **4**: 463. ♂.
Hyptiogaster macronyx (Schletterer), Kieffer, 1903, *Bull. Soc. ent. Fr.* **1903**: 94.
Hyptiogaster macronyx (Schletterer), Kieffer, 1912, Evaniidae, *Das Tierreich* **30**: 204.
Hyptiogaster macronyx (Schletterer), Tillyard, 1926, *Insects of Australia and New Zealand*: 268.
Hyptiogaster macronyx (Schletterer), Hedicke, 1939, *Hymenopterorum catalogus*, pars **11**: 49.

Length: 17 mm.

Red, dorsal side of the first segment of the gaster black and occasionally a mark round the ocelli black.

Head: Slightly wider than the thorax, rugose between the ocelli and the antennae, but smooth behind the ocelli; malar area long, about equal in length to the first antennal segment; frontal carina strong; distance between a posterior ocellus and the eye not more than half that between a posterior ocellus and the occipital carina; third antennal segment very much longer than the first, five times as long as the second, and almost as long as the fourth and fifth together; terminal flagellar segments almost twice as long as broad.

Thorax: pronotum without processes, shagreened, with transverse wrinkles along the pronotal depressions; mesonotum almost as broad as long, with transverse punctured wrinkling; scutellum regularly transversely wrinkled; mesopleura, metapleura and propodeum as in *C. grossitarsis.* Hind coxae finely transversely striated above, smooth beneath; hind trochanter with a transverse groove; hind femora short and very thick, equal in length to the hind tibia; hind tarsi as in *C. grossitarsis* (fig. 14). Hind wing with 6 hamuli.

Gaster: one and three quarter times as long as the head and thorax together, transversely wrinkled on the dorsal side of the first segment, the wrinkling continuing to the base; ovipositor very short, curved, not extending beyond the gaster.

Affinities.—Very closely allied to *C. grossitarsis*, differing chiefly in the key characters.

Specimens.—1 ♀, Australia : Brisbane, Queensland, 4.xii.1911 (*H. Hacker*) ; 1 ♀, Australia.

Type.—H. de Saussure's collection, Genf.

2. *Crassifoenus grossitarsis* (Kieffer, 1911).

Hyptiogaster grossitarsis Kieffer, 1911, *Ann. Soc. ent. Fr.* **80** : 179. ♀
H. grossitarsis Kieffer, Kieffer, 1912, Evaniidae, *Das Tierreich* **30** : 197.
H. grossitarsis Kieffer, Hedicke, 1939, *Hymenopterorum catalogus*, pars **11** : 48.

Length: 17 mm.

Red, or reddish-yellow, with the dorsum of the first segment of the gaster black, and a variable amount of black on the mesopleura, mesosternal region, the hind angle of the prescutum, central part of the scutum, on the lower angle of the metapleura, and on the propodeal spiracle.

Head : wider than the thorax, rugose-striate between the antennal insertions and the ocelli, mainly smooth behind the ocelli except for a few longitudinal wrinkles which do not reach to the occipital carina ; clypeus and inter-antennal area glabrous and separated by a very distinct epistomal suture ; malar area long, a little longer than the first antennal segment and much longer than the width of the mandible at the base ; frontal carina very strong ; distance from a posterior ocellus to the eye three-quarters as great as that between a posterior ocellus and the occipital carina ; third antennal segment half as long again as the first, four times as long as the second, and a fraction shorter than the fourth and fifth segments combined ; terminal flagellar segments only slightly longer than broad.

Thorax : pronotum without teeth, mainly smooth and shining but with shallow punctures in the pronotal depressions ; mesonotum almost as broad as long, rugosely punctured ; scutellum with scattered punctures, smooth between the punctures ; upper mesepisternum finely shagreened, lower mesepisternum rugosely punctured and separated from the upper by a line of deep punctures at which the coloration changes ; mesepimera deeply concave, smooth and shining anteriorly, but with short transverse striae posteriorly ; lower parts of the metapleura coarsely shagreened with two small deep hollows separated by a fine carina between the mid and hind coxae ; upper part of the metapleuron strongly convex, shiny on the anterior half but with fine transverse striae on the hinder half ; pits of the metapleural apophyses very deep, the propodeal spiracles very long and dark ; propodeum finely rugose with a short fine median longitudinal carina above the hind coxae. Hind coxae mainly smooth, very fine striation in the coxal depressions ; hind trochanters with a transverse groove ; hind femora short and broad, about three times as long as wide, equal in length to the hind tibia ; latter with long pubescence and a terminal pecten of short tooth-like hairs ; hind tarsi of curious conformation (fig. 14), the first four segments deeply bilobed and fitting tightly into one another, the last segment enlarged, very thick, strongly convex above, and as long as the preceding four segments together ; hind tarsal claws very large, as long as the last tarsal segment ; the latter with a mat of hair on the ventral side. Hind wing with 6 or 7 hamuli.

Gaster : one and a half times as long as the rest of the body ; dorsal surface of the first segment with transverse wrinkling which does not reach to the base of the segment ; ovipositor very short, not protruding beyond the gaster.

Affinities.—Closely allied to *C. macronyx*.

Specimens.—Type, ♀, Western Australia : Swan River (British Museum, No. 3 a.159) ; Western Australia : Roeburne, 1 ♂ (*R. E. Turner*).

6. Gen. 2. **Carinafoenus** gen. n.

Stout-bodied Gasteruptionidae, malar area short, not nearly as long as the first antennal segment but equal in length to or shorter than the width of the mandible at the base; hind angles of the head well marked; vertex with at least a slight trace of a transverse furrow; frontal carina strong; fourth antennal segment about equal in length to the third, all segments very elongate. Pronotum sometimes with processes, the mesonotum much longer than broad if processes are present; hind trochanter with a very distinct transverse groove, hind femur without a lobe differentiated off basally; hind tibia longer than the femur; hind tarsi symmetrical, but sometimes sexually dimorphic, so that the segments are of different proportions in the male and the female; in sexually dimorphic species the hind claws of the female are very enlarged and as long as the fifth tarsal segment. Fore wing with two closed discoidal cells and the cubitus springing from the basal vein (fig. 1); hind wing with 5–7 hamuli. Ovipositor long, protruding far beyond the end of the gaster, but never longer than the gaster; dorsum of the first segment of the gaster always to some extent sculptured, never quite smooth.

Type-species: *Foenus rufus* Westwood, 1841, original designation.

5 species, Australia.

(*a*) *Key to the species of* Carinafoenus.

1. Pronotum with processes; mesonotum elongate . . . . 2.

–. Pronotum without processes; mesonotum about as broad as long . . 3.

2. Length 23 mm.; body entirely red; lower pronotal process not as strong as the upper process . . . . 1. **C. flavosignatus** (Kieffer)

–. Length 17–20 mm.; body red with the dorsal side of the first segment of the gaster black; pronotal processes equally strongly developed 2. **C. humeralis** (Schletterer)

3. Frontal carina viewed from the side with a strong triangular tubercle at the ventral end (fig. 8); head coarsely reticulate; ovipositor two-thirds as long as the gaster, about equal in length to the hind tibia and tarsus combined . . . . 3. **C. arenicola** (Turner)

–. Frontal carina without a strong tubercle at the ventral end (fig. 9); head closely punctured; ovipositor three-quarters as long as the gaster, longer than the hind tibia and tarsus combined . . . . 4.

4. Hind coxae strongly transversely striate; hind claws small, not nearly as long as the fifth tarsal segment; pterostigma yellow in the middle 4. **C. rufus** (Westwood)

–. Hind coxae only very finely sculptured; hind claws large, as long as the fifth tarsal segment; pterostigma brown 5. **C. crassiceps** (Schletterer)

(*b*) Descriptions of the species of *Carinafoenus*.

1. *Carinafoenus flavosignatus* (Kieffer, 1911).

Odontofoenus flavosignatus Kieffer, 1911, *Ann. Soc. ent. Fr.* **80**: 177. ♀

Hyptiogaster flavosignata (Kieffer), Kieffer, 1912, Evaniidae, *Das Tierreich*, **30**: 196.

H. flavosignata (Kieffer), Hedicke, 1939, *Hymenopterorum catalogus*, pars **11**: 48.

Length: 23 mm.

Entirely light red, except the teeth of the mandibles and the tarsal claws dark.

Head: broader than the thorax, with a shallow transverse furrow from eye to eye behind the ocelli; inter-antennal area and clypeus rather yellow, glabrous, diffusely and finely punctured; malar area short, equal in length to the second antennal segment; frontal carina strong ; hind angles of the head well marked ; distance from a posterior ocellus to the occipital carina twice that between a posterior ocellus and the eye ; third antennal segment three times as long as the second, fourth equal in length to the third ; terminal flagellar segments very elongate.

Thorax : pronotum with an antero-dorsal and an antero-ventral process on each side, the upper processes stronger than the lower ones, almost smooth ; mesonotum much longer than broad, closely punctured with a tendency to transverse wrinkling on the anterior part of the prescutum ; puncturation of the scutum stronger and tending to reticulation ; mesopleura almost smooth ; propodeum very finely and closely punctured with a fine central carina. Hind coxae transversely striated dorsally ; hind trochanter with a transverse groove ; hind tibiae with short sparse spiny hairs among ordinary pubescence ; hind tarsi strongly sexually dimorphic, male with the metatarsus nearly as long as the four following segments together (fig. 11), female with the metatarsus very much shorter than the four succeeding segments (fig. 10) ; hind claws very large in the female. Hind wing with 7 hamuli in the male, 6 in the female.

Gaster : dorsal side of the first segment transversely reticulately wrinkled ; ovipositor one-quarter as long as the gaster, valves black with the apical halves yellow.

Affinities.—Closely allied to *C. humeralis*.

Specimens.—Type ♀, WESTERN AUSTRALIA : Warooka, 13.ii.1909 (*G. F. Berthoud*) (British Museum, No. 3 a. 180) ; 1 ♂, data as for type.

2. *Carinafoenus humeralis* (Schletterer, 1889).

Gasteruption humerale Schletterer, 1889, *Ann. naturh. (Mus.) Hofmus. Wien* **4** : 459. ♂, ♀.
Hyptiogaster humeralis (Schletterer), Kieffer, 1903, *Bull. Soc. ent. Fr.* **1903** : 94.
Eufoenus humeralis (Schletterer), Szépligeti, 1903, *Ann. hist.-nat. Mus. hung.* **1** : 365.
Odontofoenus humeralis (Schletterer), Kieffer, 1910, *Ann. Soc. ent. Fr.* **79** : 77.
Hyptiogaster humeralis (Schletterer), Kieffer, 1912, Evaniidae, *Das Tierreich* **30** : 197.
H. humeralis (Schletterer), Hedicke, 1939, *Hymenopterorum catalogus*, pars **11** : 48.

Length : 17–20 mm.

Light or dark red, the dorsum of the first segment of the gaster black, mandibular teeth, scutellar pockets, and ventral parts of the mesopleura dark.

Head : scarcely broader than the thorax, hind angles well marked, with a transverse furrow behind the ocelli, and finely punctured on the vertex. Clypeus and inter-antennal area glabrous and shining, more finely punctured than in *C. flavosignatus* ; epistomal suture very distinct ; malar area equal in length to the second antennal segment ; frontal carina strong. Distance from a posterior ocellus to the occipital carina twice that between a posterior ocellus and the eye. Fourth antennal segment about equal in length to the third.

Thorax : pronotum with antero-dorsal and antero-ventral teeth, these equally strongly developed ; pronotum smooth ; mesonotum much longer than broad, reticulately punctured ; mesopleura almost smooth ; propodeum finely reticulately punctured, with a fine median carina. Hind coxae transversely striated in the coxal depressions ; hind trochanter with a transverse groove ; hind tibiae with short sparse spiny hairs among the ordinary fine pubescence ; hind tarsi sexually dimorphic, the male with the fifth segment about equal in length to the second, third, and fourth segments together (fig. 12), and the female with the fifth segment very much shorter than these together (fig. 13) ; hind claws not enlarged. Hind wing with 6 hamuli.

Gaster : transversely wrinkled on the dorsum of the first segment ; ovipositor exserted, shorter than the gaster, valves black with the apices white.

Affinities.—Close to *C. flavosignatus* ; these two species form a small group quite distinct from the rest of the genus in having a toothed pronotum and an elongate mesonotum.

Specimens.—1 ♂ and 1 ♀, South Australia.

3. *Carinafoenus arenicola* (Turner, 1918).

Hyptiogaster arenicola Turner, 1918, *Ann. Mag. nat. Hist.* (9) **1** : 408. ♂, ♀.
H. arenicola Turner, Hedicke, 1939, *Hymenopterorum catalogus*, pars **11** : 47.

Length : ♂ 16–17 mm., ♀ 14–16 mm., ovipositor 6 mm.

Red, usually with the head dark and the thorax and gaster fuscous to a variable extent, ovipositor valves black with the apical two-fifths yellow.

Head : broader than the thorax, coarsely reticulate, the furrow on the vertex only faintly marked in the reticulation ; hind angles of the head well marked ; clypeus and inter-antennal area very finely punctured, with very short pubescence ; malar area a little longer than the second antennal segment ; frontal carina strong and raised into a triangular tubercle at the ventral end between the antennal insertions. Distance from the eye to a posterior ocellus greater than half that between a posterior ocellus and the occipital carina. Third antennal segment a fraction longer than the fourth, one and a half times as long as the first ; terminal flagellar segments elongate.

Thorax : pronotum without processes and with only a trace of a V-shaped depression on each side ; mesonotum nearly as broad as long, closely and coarsely punctured with a tendency to transverse wrinkling on the anterior border of the prescutum ; mesepimeron with a double row of large punctures ; propodeum moderately punctured and without a median carina. Hind coxae only faintly striated dorsally ; hind trochanter with a transverse groove ; hind tibiae pitted and with very short sparse spiny hairs among the ordinary pubescence, only visible under high power ; hind metatarsus rather broader than the succeeding segments and nearly equal in length to these combined ; claws of the hind leg small, about half as long as the last tarsal segment. Hind wing with 5 hamuli.

Gaster : very finely sculptured on the dorsum of the first segment ; ovipositor exserted, two-thirds as long as the gaster, or equal in length to the hind tibia and tarsus combined.

Affinities.—With *C. rufus* and *C. crassiceps* rather than *C. humeralis* ; it is readily distinguishable, however, from other *Carinafoenus* by the tuberculate character of the frontal carina.

Specimens.—Type ♀, S.W. AUSTRALIA : Yallingup, 23.xii.1913–23.i.1914 *R. E. Turner*) (British Museum, No. 3a. 154) ; allotype (labelled as cotype by R. E. Turner) : ♂, data as for type ; S.W. AUSTRALIA : Yallingup, 23.xii.1913–23.i.1914, 7♀ and 11 ♂ (*R. E. Turner*) ; WESTERN AUSTRALIA : Yanchep, 32 miles North of Perth, 24.xi.1935–23.i.1936, 11 ♀ and 2♂ (*R. E. Turner*).

Habits.—Has been observed in numbers flying low over sand-hills on the coast.

4. *Carinafoenus rufus* (Westwood, 1841).

Foenus rufus Westwood, 1841, *Ann. Mag. nat. Hist.* **7** : 537. ♂.
Gasteruption rufum (Westwood), Schletterer, 1889, *Ann. naturh. (Mus.) Hofmus. Wien* **4** : 464.
Hyptiogaster rufa (Westwood), Kieffer, 1903, *Bull. Soc. ent. Fr.* **1903** : 94.
Hyptiogaster macrochela Kieffer, 1911, *Ann. Soc. ent. Fr.* **80** : 180.
Hyptiogaster rufa (Westwood), Kieffer, 1912, Evaniidae, *Das Tierreich* **30** : 202.
Hyptiogaster macrochela Kieffer, Kieffer, 1912, Evaniidae, *Das Tierreich* **30** : 201.
Hyptiogaster rufa (Westwood), Hedicke, 1939, *Hymenopterorum catalogus*, pars **11** : 49.

Length : ♂ 11 mm., ♀ 16 mm., ovipositor 8 mm.

Largely dark red ; head black with clypeus red in the male, black on the mesonotum in the male, line along the dorsum of the gaster and the mandibular teeth black or brown.

Head : wider than the thorax, with well-marked hind angles, finely and closely punctured ; vertex with a narrow short ill-defined transverse groove behind the ocelli ; clypeus and inter-antennal area very finely pubescent, closely punctured ; epistomal suture not very distinct ; malar area slightly longer than the second antennal segment ; frontal carina distinct, not produced into a ventral tubercle ; distance from a posterior ocellus to the eye a little greater than half that between a posterior ocellus and the occipital carina. Third antennal segment a little longer than the first, about equal in length to the fourth (fig. 2).

Thorax : pronotum without processes, finely punctured and with a V-shaped depression on each side ; mesonotum nearly as broad as long, coarsely reticulate in the male, transversely wrinkled and punctured in the female ; mesepimera transversely wrinkled ; propodeum finely punctured, without trace of a fine median longitudinal carina. Hind coxae transversely striated dorsally ; hind trochanter with a transverse groove ; hind tibiae finely pitted, without or with only very short sparse spiny hairs ; hind tarsi symmetrical, the metatarsus a little thicker than the succeeding segments, and a little shorter than these combined ; claws normal. Hind wing with 5 hamuli.

Gaster : first segment finely punctured at the base, not wrinkled ; ovipositor about three-quarters as long as the gaster, longer than the hind tibia and tarsus together.

Affinities.—Closely allied to *C. crassiceps* and *C. arenicola*, though from the latter it can easily be distinguished on the frontal carina ; these three species together differ from the others of the genus in the subquadrate and not elongate mesonotum, and in the simple pronotum ; the head, too, is always strongly sculptured, and not smooth and shining as in *C. flavosignatus* and *C. humeralis*.

Specimens.—Cotype : ♀, S.E. AUSTRALIA (British Museum), (F. Smith collection). 1 ♀, S.E. AUSTRALIA. Kieffer's type *H. macrochela* was described from Victoria.

5. *Carinafoenus crassiceps* (Schletterer, 1889).

Gasteruption crassiceps Schletterer, 1889, *Ann. naturh.* (*Mus.*) *Hofmus. Wien* **4** : 462. ♂, ♀.
Hyptiogaster crassiceps (Schletterer), Kieffer, 1903, *Bull. Soc. ent. Fr.* **1903** : 93.
Eufoenus crassiceps (Schletterer), Szépligeti, 1903, *Ann. hist.-nat. Mus. hung.* **1** : 365.
Hyptiogaster crassiceps (Schletterer), Kieffer, 1912, Evaniidae, *Das Tierreich* **30** : 203.
H. crassiceps (Schletterer), Hedicke, 1939, *Hymenopterorum catalogus*, pars **11** : 48.

Length : 15–20 mm.

Reddish-yellow, with brown to black marking dorsally, more developed in the male than the female.

Head : broader than the thorax, moderately closely punctured, hinder part short, the angles well marked ; malar area nearly twice as long as the second antennal segment ; frontal carina strong, very slightly produced at the ventral end. Third antennal segment in the male a fraction longer than the fourth, equal in length to the fourth in the female ; third antennal segment five times as long as the second in the male, four times as long in the female ; flagellar segments elongate.

Thorax : pronotum without processes, coarsely shagreened, striated in the depressions ; mesonotum nearly as broad as long, strongly transversely rugose, punctured between the wrinkles ; mesopleura coarsely shagreened, upper parts of the metapleura transversely striate ; propodeum strongly and irregularly rugose. Hind coxae very lightly sculptured, not strongly striate as in *C. rufus* ; hind trochanter with a transverse groove ; hind metatarsi a little shorter than the four following segments together, the claws enlarged and about as long as the last tarsal segment, this feature distinguishing the species from *C. rufus*. Hind wing with 5 hamuli.

Gaster : very lightly sculptured on the dorsal side of the first segment ; ovipositor exserted, about half as long as the whole body, the apical halves of the valves white.

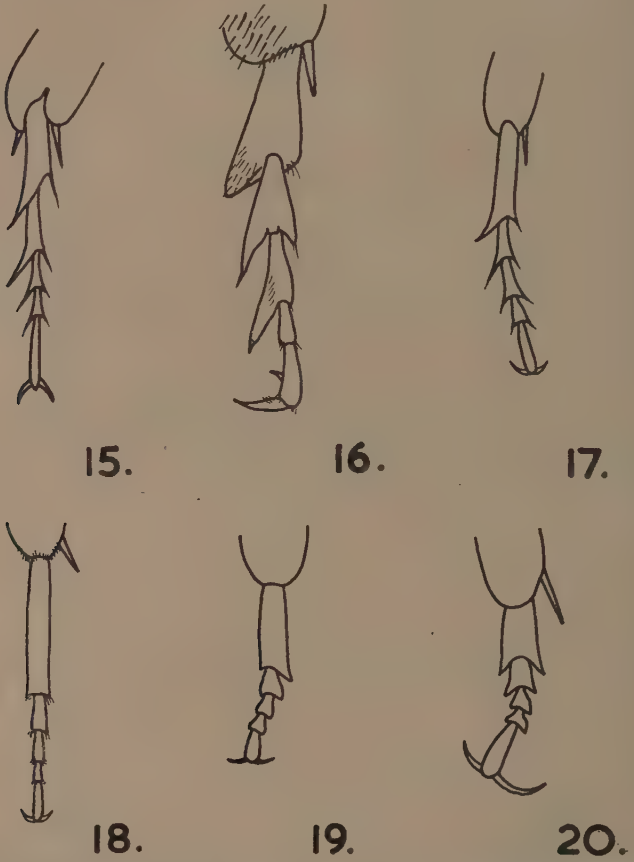
Affinities.—Closely related to *C. rufus* ; in the character of the frontal carina it is somewhat intermediate between *C. rufus* and *C. arenicola*.

Specimens.—1 ♀, WESTERN AUSTRALIA : Dedari, 40 miles west of Coolgardie, 11–21.i.1936 (*R. E. Turner*).

Type from South Australia, probably in Hofmuseum, Vienna.

7. Gen. 3. HYPTIOGASTER Kieffer, 1903.

Hyptiogaster Kieffer, 1903, *Bull. Soc. ent. Fr.* **1903** : 93.
Eufoenus Szépligeti, 1903, *Ann. hist.-nat. Mus. hung.* **1** : 365.
Hyptiogaster Kieffer, Kieffer, 1904, *Bull. Soc. Metz* **23** : 14.
Hyptiogaster Kieffer, Bradley, 1908, *Trans. Amer. ent. Soc.* **34** : 108.
pro parte Odontofoenus Kieffer, 1910, *Ann. Soc. ent. Fr.* **79** : 77.



FIGS. 15–20.—*Hyptiogaster*. Hind tarsus, dorsal. (15) *H. brevithorax* Kieffer; (16) *H. asymmetrica* Turner; (17) *H. darwinii* Westwood; (18) *H. floricola* Turner; (19) *H. nitidiuscula* Turner; (20) *H. inaequalis* Turner.

Hyptiogaster Kieffer, Kieffer, 1911, *Ann. Soc. ent. Fr.* **80** : 177.
pro parte Aulacofoenus Kieffer, 1911, *Ann. Soc. ent. Fr.* **80** : 177.
pro parte Hemifoenus Kieffer, 1911, *Ann. Soc. ent. Fr.* **80** : 182.
pro parte Trigonofoenus Kieffer, 1911 (*partim*), *Ann. Soc. ent. Fr.* **80** : 177.
pro parte Gasteruption Latreille, Kieffer, 1912, Evaniidae, *Das Tierreich* **30**.
Hyptiogaster Kieffer, Kieffer, 1912, Evaniidae, *Das Tierreich* **30** : 194.

pro parte Pseudofoenus Kieffer, 1912 (*partim*), Evaniidae, *Das Tierreich* **30** : 211.
pro parte Aulacofoenus Kieffer, Kieffer, 1912, Evaniidae, *Das Tierreich* **30** : 193.
pro parte Hemifoenus Kieffer, Kieffer, 1912, Evaniidae, *Das Tierreich* **30** : 192.
Hyptiogaster Kieffer, Turner, 1918, *Ann. Mag. nat. Hist.* (9) **1** : 408–412.
pro parte Hemifoenus Kieffer, Brues, 1922, *Psyche, Camb., Mass.* **29** : 11.
Hyptiogaster Kieffer, Hedicke, 1939, *Hymenopterorum catalogus, pars* **11** : 47.
pro parte Gasteruption Latreille (*partim*), Hedicke, 1939, *Hymenopterorum catalogus*, pars **11** : 40.
pro parte Aulacofoenus Kieffer, Hedicke, 1939, *Hymenopterorum catalogus*, pars **11** : 50.
pro parte Hemifoenus Kieffer, Hedicke, 1939, *Hymenopterorum catalogus*, pars **11** : 50.
pro parte Trigonofoenus Kieffer (*partim*), Hedicke, 1939, *Hymenopterorum catalogus*, pars **11** : 42.

Stout-bodied Gasteruptionidae; malar area shorter than the first antennal segment; hind angles of the head usually not well-marked (figs. 21–25); frontal carina most commonly absent, sometimes present; fourth antennal segment very much shorter than the third, the terminal flagellar segments frequently almost quadrate. Pronotum without processes; mesonotum as broad as or very nearly as broad as long, never distinctly elongate. Form of the thorax never very elongate, always deep, and frequently very nearly as high as long so as to appear almost quadrate in side view. Hind trochanter in almost every case without a transverse groove, hind femur without a lobe differentiated off basally; hind tibia longer than the hind femur, in some cases only just so; hind tarsi usually symmetrical, but sometimes very markedly asymmetrical, sexual dimorphism unusual; hind claws normally small, but as long as the last tarsal segment in some species. Fore wing with two closed discoidal cells and the cubitus springing from the basal vein (fig. 1); hind wing with 3–4 hamuli (5 occasionally in *H. asymmetrica*). Ovipositor always very short, hidden, never extending beyond the apex of the gaster.

Type-species: *Foenus australis* Westwood, 1835, subsequent designation.

23 species: Australasian (Australia, Fiji, New Hebrides, but not New Zealand), and Neotropical (Brazil, Argentina).

(*a*) Key to the species of *Hyptiogaster*.

1. Strong frontal carina present between the antennae . . . . 2.
–. Frontal carina absent . . . . 8.
2. Frontal carina so strongly developed that in side view it appears as a blunt horn above the antennal insertions (fig. 7); hind tarsal segments asymmetrical and deeply incised with the outer teeth greatly developed (fig. 16), so much so in the female that the fourth segment is hidden by the third in outer view . . . 1. **H. asymmetrica** Turner
–. Frontal carina simple, not horn-like; hind tarsal segments symmetrical 3.
3. Hind trochanter divided into two parts by a transverse groove; hind coxae distinctly transversely striated above 2. **H. fallax** (Schletterer)
–. Hind trochanter simple; hind coxae smooth or only microscopically striate . . . . 4.
4. Head very strongly contracted behind the eyes (fig. 21), so that it is very nearly twice as broad as long; propodeum with a number of transverse carinae, one usually very strong; length 7·5 mm. 3. **H. ferruginea** sp. n.
–. Head not strongly contracted behind the eyes (fig. 22), not nearly twice as broad as long; propodeum without transverse carinae; length 8·5–15 mm. . . . . 5.
5. Body largely black or dark reddish-black; propodeum with a short median longitudinal carina above the hind coxae; hind claws small, much shorter than the fifth tarsal segment; terminal flagellar segments elongate; gaster long and slender . . . . 6.

–. Body almost entirely bright red; propodeum without a short median carina; hind claws large, as long as or almost as long as the last tarsal segment; terminal flagellar segments subquadrate; gaster short and stout . . . . 7.

6. Mesonotum coarsely and evenly punctured; hind tarsi white except for the bases of the metatarsi black; pronotum largely black; head usually entirely black, occasionally clypeus fuscous; mid tarsi white basally, darkening to black apically . . . 4. **H. patellata** (Westwood)
–. Mesonotum transversely wrinkled; hind tarsi red; pronotum entirely red; head black with the clypeus red; first four segments of the mid tarsi red, terminal segment dark . . . . 5. **H. australis** (Westwood)

7. Mesonotum with small widely spaced punctures, the areas between the punctures smooth and shining; last segment of the hind tarsus much shorter than the first (fig. 19); third antennal segment three and a half times as long as the second (fig. 3) . . 6. **H. nitidiuscula** Turner
–. Mesonotum coarsely rugosely punctured with a tendency to reticulate wrinkling, no smooth areas between the uneven punctures; last segment of the hind tarsus equal in length to the first (fig. 20); third antennal segment four times as long as the second (fig. 4) 7. **H. inaequalis** Turner

8. Hind trochanter divided into two by a transverse groove; prescutum red with a median longitudinal black line and the limiting prescutal suture black; distribution Neotropical . . . . 9.
–. Hind trochanter simple; prescutum black or red; or black with red borders, but without a characteristic anchor-shaped black mark on a red ground; distribution Australasian . . . . 10.

9. Wings colourless; scutum without a distinct deep median longitudinal furrow; prescutum strongly and irregularly rugose, tending to transverse rugosity on the median black line; hind coxae not transversely striated . . . . 8. **H. szépligetii** Kieffer
–. Wings smoky brownish; scutum with a deep distinct median longitudinal furrow; prescutum strongly transversely wrinkled; hind coxae transversely striated . . . . 9. **H. infumata** (Schletterer)

10. Hind tarsi asymmetrical so that all or some segments have a strongly developed terminal tooth on the outer side (figs. 15 and 17) . . . 11.
–. Hind tarsi symmetrical, without strongly developed teeth on any of the segments (e.g., fig. 18) . . . . 13.

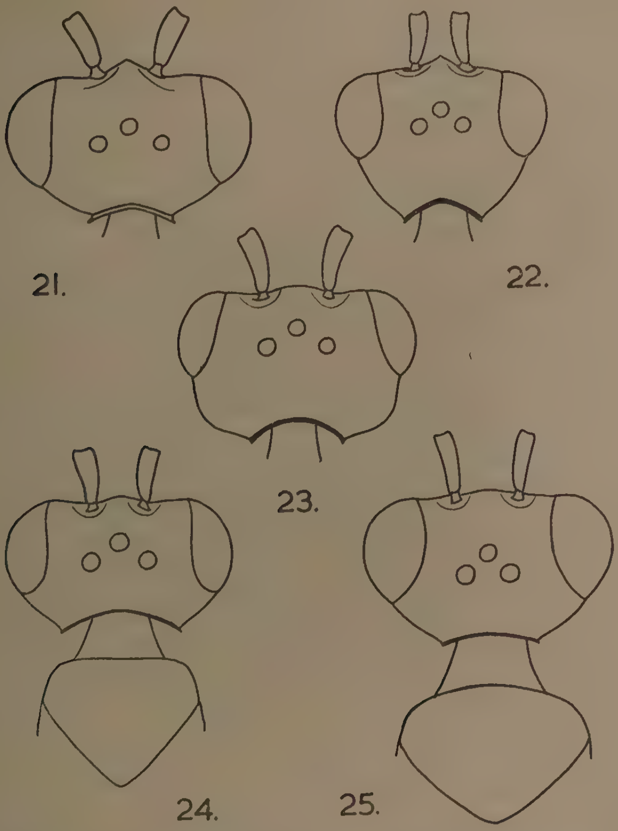
11. Asymmetry of the hind tarsi very strong, the third segment clearly asymmetrical (fig. 15); mesonotum with scattered shallow punctures, finely shagreened between the punctures; hind femora and tibiae short and broad; hind wing with 4 hamuli; length 10–11 mm. 12
–. Asymmetry of the hind tarsi not very strong, the third segment symmetrical (fig. 17); mesonotum closely punctured, coarsely shagreened between the punctures; hind femora and tibiae not unusually short and broad; hind wing with 3 hamuli; length 6 mm 10. **H. darwinii** (Westwood)

12. Thorax subquadrate when viewed from the side; longitudinal scutellar furrows complete; hind tibia only very slightly longer than the hind femur . . . . 11. **H. brevithorax** (Kieffer)
–. Thorax clearly slightly elongate viewed from the side; longitudinal scutellar furrows interrupted; hind tibia distinctly longer than the hind femur . . . . 12. **H. interrupta** sp. n.

13. Hind tarsi white except the last segment dark, and the extreme bases of the metatarsi black ; length 15·5 mm. . . . 13. **H. plicata** (Schletterer)

–. Hind tarsi unicolorous red, fuscous, or blackish ; length 4–11 mm. . 14.

14. All segments of the gaster with long outstanding pubescence ; hind angles of the head well marked (fig. 23) . . . . . 14. **H. pilosa** Kieffer



FIGS. 21–25.—*Hyptiogaster*. Dorsal view of the head. (21) *H. ferruginea* sp. n. ; (22) *H. patellata* Westwood ; (23) *H. pilosa* Kieffer ; (24) *H. microcephala* sp. n. ; (25) *H. ritae* Cheesman. In figs. 24 and 25 the prescutum is shown also.

–. Gaster without long outstanding pubescence except occasionally on the terminal segments ; hind angles of the head not well marked so that the head is contracted behind the eyes (fig. 25). (In *H. antennalis* the hind angles of the head are nearly as well marked as in *H. pilosa*, but there is a short median longitudinal carina on the propodeum which is missing in *H. pilosa*) . . . . 15.

15. Prescutum and lateral parts of the scutum very raised and convex, the mesonotal furrows deep; prescutum crossed by strong curved parallel transverse unpunctured wrinkles, these continuing on to the parapsides; head and thorax light reddish-yellow; length 7 mm.; Fiji Islands . . . . 15. **H. extranea** Turner

–. Mesonotum not strongly convex and not crossed by parallel ridges; mesonotal furrows not very deep; head and thorax not entirely reddish-yellow, but largely black; length 4–6 mm. or 8–10 mm.; Australia or New Hebrides . . . . 16.

16. Length 8–10 mm.; propodeum with a short median longitudinal carina above the hind coxae; mesonotum strongly rugose; gaster nearly twice as long as head and thorax, not greatly expanded towards the apex when viewed laterally . . . . 17.

–. Length 4–6 mm.; propodeum without a short median carina above the hind coxae; mesonotum rugose or evenly punctured; gaster short, at most one and a half times as long as the head and thorax, and expanded towards the apex when viewed laterally . . . . . 19.

17. Hind angles of the head very nearly as strong as in *H. pilosa* (fig. 23); gaster entirely black . . . . 16. **H. antennalis** (Schletterer)

–. Hind angles of the head not well marked, the head contracted behind the eyes (figs. 24 and 25); gaster with each segment in part reddish or yellowish . . . . 18.

18. Distance between the posterior ocelli a little greater than that between a posterior ocellus and the eye (fig. 24); anterior border of the prescutum straight, the angles well marked (fig. 24); head coarsely shagreened with radiating striae round each ocellus; hind metatarsus three times as long as broad; hind femora short and thick, about four and a half times as long as broad; anterior discoidal cell three-cornered, the cubitus springing from the middle of the basal vein; Australia . . . . 17. **H. microcephala** sp. n.

–. Distance between the posterior ocelli smaller than that between a posterior ocellus and the eye (fig. 25); anterior border of the prescutum evenly curved, the angles not well marked (fig. 25); head with scattered punctures, and occasionally transversely striate behind the ocelli, no radiating striae; hind metatarsus five times as long as broad; hind femora and tibiae long and narrow, about six times as long as broad; anterior discoidal cell four-cornered, the cubitus arising from the basal vein nearer to the median vein than to the subcosta; New Hebrides . . . . 18. **H. ritae** Cheesman

19. Mesepimera transversely wrinkled and extending to the ventral side of the thorax; head entirely black; third antennal segment three and a half times as long as the second, hardly at all shorter than the fourth and fifth segments combined; hind femora with long outstanding pubescence; terminal flagellar segments nearly quadrate 19. **H. floricola** Turner

–. Mesepimera coarsely shagreened, not concave and not reaching the ventral side of the thorax; head with the clypeus and a small mark round each eye red or fuscous; third antennal segment three times as long as the second, distinctly shorter than the fourth and fifth segments together; hind femora without long outstanding pubescence; terminal flagellar segments one and a half times as long as broad . . . . 20. **H. minima** Turner

Three species that the author was unable to examine or have examined for him, have been omitted from the above key, but descriptions of these three species taken from the originals are given later on p. 382. The species in question are *H. deletangi* (Schletterer), *H. crassitarsis* Kieffer, and *H. flavinervis* Kieffer.

(*b*) Descriptions of the species of *Hyptiogaster*.

1. *Hyptiogaster asymmetrica* Turner, 1918.

Hyptiogaster asymmetrica Turner, 1918, *Ann. Mag. nat. Hist.* (9) **1** : 409. ♂, ♀.
H. asymmetrica Turner, Hedicke, 1939, *Hymenopterorum catalogus*, pars **11** : 47.

Length : ♂ 20 mm., ♀ 18 mm.

Dark red, sometimes with head and gaster nearly black.

Head : broader than the thorax, closely punctured on the vertex, face finely and closely punctured ; most of the head with long outstanding silvery pubescence ; malar area no longer than the second antennal segment ; frontal carina very strongly developed (fig. 7), so that in side view it appears as a blunt horn above the bases of the antennae. Distance from the eye to a posterior ocellus almost as great as that between a posterior ocellus and the hind margin of the head. Third antennal segment a little longer than the first, four times as long as the second, and very nearly as long as the fourth and fifth segments combined ; terminal flagellar segments longer than broad.

Thorax : pronotum without teeth, nearly smooth, and with a Y-shaped depression on either side ; mesonotum about as broad as long, coarsely rugose-reticulate ; scutellum with raised transverse wrinkles ; mesepisterna and lower parts of the metapleura very finely punctured ; upper parts of the metapleura with parallel ridges ; mesepimera deeply concave and largely smooth ; propodeum reticulate with a fine median carina. Hind coxae mat, with fine striation in the dorsal depressions ; hind trochanter with a transverse groove; hind tibiae with spiny hairs as well as ordinary pubescence ; hind tarsi asymmetrical (fig. 16), short and thick, with a long tooth developed on the outer side of the end of each segment; in the female in side view the tooth is very large on the third segment and completely obscures the fourth ; latter very small and not asymmetric ; metatarsus a little longer than the following two segments together, but distinctly shorter than the three following segments together ; each tarsal segment except the last much narrower than the preceding one ; claws slightly enlarged, only a little shorter than the fifth tarsal segments. Hind wing with 4 hamuli, some individuals with 5.

Gaster : first segment finely rugulose above ; ovipositor short, curved, not extending beyond the apex of the gaster.

Affinities.—A very curious and isolated species, with no obvious affinity to others of the genus ; the strong horn-like frontal carina is unique, and the species is further unusual in possessing a transverse groove on the posterior trochanter. The asymmetry of the hind tarsi is also a very characteristic feature, but there is no doubt that this has been derived quite independently of the tarsal asymmetry of the *H. brevithorax*-group. In general build, the strong frontal carina and the grooved hind trochanter, *H. asymmetrica* approaches *Carinafoenus*, but it is included here under *Hyptiogaster* on account of the lengths of the antennal segments and the short, hidden, ovipositor.

Specimens.—Type ♀, South-west Australia : near Cape Naturaliste, Yallingup, 14.ix–31.x.1913 (*R. E. Turner*) (British Museum, No. 3 a. 155) ; allotype (labelled as cotype by R. E. Turner) : ♂, data as for type ; paratype : 7 ♂, 11 ♀, data as for type ; 2 ♀, locality as for type, date xi.1913.

2. *Hyptiogaster fallax* (Schletterer, 1889).

Gasteruption fallax Schletterer, 1889, *Ann. naturh.* (*Mus.*) *Hofmus. Wien* **4** : 461. ♂.
Hyptiogaster fallax (Schletterer), Kieffer, 1903, *Bull. Soc. ent. Fr.* **1903** : 94.
H. fallax (Schletterer), Kieffer, 1912, Evaniidae, *Das Tierreich* **30** : 201.
H. fallax (Schletterer), Hedicke, 1939, *Hymenopterorum catalogus*, pars **11** : 48.

Length : ♂, type 14·5 mm. (Schletterer and Kieffer give 16–18 mm.).

Black with the pronotum, meso- and metapleura, the propodeum, and undersides of the hind coxae red ; tarsi fulvous.

Head : short and broad, strongly contracted behind the eyes ; vertex finely shagreened ; malar area very short ; frontal carina present and strong. Third antennal segment four times as long as the second, one-third as long again as the fourth ; terminal flagellar segments missing from the type.

Thorax : pronotum without processes ; mesonotum strongly rugose, but with a distinct tendency to transverse striation, especially on the prescutum ; propodeum moderately finely punctured and rugose, and with a fine median longitudinal carina above the hind coxae. Hind coxae shining and finely transversely striate dorsally ; hind trochanter with a transverse groove ; hind tarsi symmetrical, the metatarsus shorter than the three following segments together, and equal in length to the last three segments combined ; fifth hind tarsal segment equal in length to the third ; metatarsus twice as long as the second segment. Hind claws small. Hind wing with 3 hamuli.

Specimens.—Type, ♂ (Berlin), examined by Dr. Bischoff for the author ; locality : AUSTRALIA : Queensland.

3. **Hyptiogaster ferruginea** sp. n.

Length : 7·5 mm.

Dull reddish-yellow, apex of the gaster, most of the head, and the antennae except for the scapes, fuscous.

Head : a little wider than the thorax, very strongly contracted behind the eyes (fig. 21), occipital carina very strong ; vertex shining, almost smooth but with fine shallow diffuse puncturation ; clypeus shining, smooth and glabrous ; malar area exceedingly short, barely half as long as the second antennal segment ; frontal carina present. Distance between the posterior ocelli one and a half times as great as that between a posterior ocellus and the eye (fig. 21) ; distance from a posterior ocellus to the eye a little more than half that between a posterior ocellus and the occipital carina. Third antennal segment a little longer and narrower than the first, three and a half times as long as the second, and a little shorter than the fourth and fifth segments combined ; terminal flagellar segments a little longer than broad.

Thorax : pronotum without processes, nearly smooth and shining, but lightly rugose in the pronotal depressions ; mesonotum almost as broad as long, with large deep close and regular puncturation, the narrow raised areas between the punctures smooth and shining ; median area of the scutellum convex and strongly punctured, the lateral scutellar grooves well marked with irregular rows of punctures ; mesepisterna and metapleura coarsely shagreened, the mesepimera deeply concave, shining, the dorsal halves with fine transverse carinae ; propodeum rugose with a number of fine transverse carinae, one of them usually longer and stronger than the rest, the carinae nearest the hind coxae connected by a short strong median longitudinal carina. Hind coxae mainly smooth and shining but with very fine transverse striations in the shallow coxal depressions ; hind trochanter without a transverse groove ; hind femora and tibiae slender, the tibiae with short spiny hairs among the ordinary pubescence ; hind tarsi symmetrical, the metatarsus broader than the following segments, equal in length to these together in the female, a little shorter than these together in the male ; hind claws normal.

Gaster : very expanded towards the end in the female, not greatly expanded in the male ; dorsum of the first segment smooth and shining ; ovipositor very short and hidden, not protruding beyond the apex of the gaster.

Affinities.—The possession of a frontal carina and the simple character of the hind tarsi indicate relationship with the *H. australis–H. patellata* group ; the species is however very much smaller than these and has a very broad and strongly contracted head quite different from that in the *H. australis*-group (cf. figs. 21 and 22). Aside from the possession of the frontal carina this species shows some points of resemblance with the *H. ritae*-group ; it is in fact a form rather intermediate between the *H. ritae* and *H. australis* groups.

Specimens.—Type : ♀, AUSTRALIA : Mackay, Queensland, 1907 (*R. E. Turner*) (in the collection of the British Museum (Natural History)). Paratypes : 1 ♂, locality as for type, 1910 (*R. E. Turner*) ; 1 ♀, locality as for type, 1891 (*G. Turner*).

4. *Hyptiogaster patellata* (Westwood, 1851).

Foenus patellatus Westwood, 1851, *Trans. ent. Soc. Lond.* **2** (1) : 221. ♂.
Gasteruption patellatum (Westwood), Schletterer, 1889, *Ann. naturh.* (*Mus.*) *Hofmus. Wien* **4** : 458.
Hyptiogaster microchela Kieffer, 1911, *Ann. Soc. ent. Fr.* **80** : 181.
Gasteruption patellatum (Westwood), Kieffer, 1912, Evaniidae, *Das Tierreich* **30** : 338.
Hyptiogaster microchela Kieffer, Kieffer, 1912, Evaniidae, *Das Tierreich* **30** : 202.
Gasteruption patellatum (Westwood), Hedicke, 1939, *Hymenopterorum catalogus*, pars **11** : 40.
Hyptiogaster microchela Kieffer, Hedicke, 1939, *Hymenopterorum catalogus*, pars **11** : 49.

Length : 14–15 mm.

Black or fuscous with scutellum, parapsides, ventral parts of the mesopleura, sides of the gaster, and occasionally some of the pronotum and mesonotum, red ; head black, occasionally clypeus fuscous ; legs fuscous, hind tarsi except the bases of the metatarsi, and the front and mid metatarsi white.

Head : prolonged behind the ocelli and gently contracted (fig. 22) ; occipital carina strong ; smooth and dull, the front with silvery pubescence ; clypeus smooth with the anterior tentorial pits and the epistomal suture well marked ; malar area equal in length to the second antennal segment ; frontal carina strong, stronger than in *H. australis* ; distance between the posterior ocelli very slightly greater than that between a posterior ocellus and the eye ; that between a posterior ocellus and the eye less than half that between a posterior ocellus and the occipital carina (fig. 22). Third antennal segment longer than the first, nearly five times as long as the second, and nearly as long as the fourth and fifth segments together (fig. 6) ; terminal flagellar segments elongate.

Thorax : pronotum without processes, very finely punctate, V-shaped depressions very shallow ; mesonotum almost as broad as long, rugosely punctured as the scutellum ; mesopleura finely punctured ; propodeum finely reticulate with a short fine median longitudinal carina above the hind coxae. Hind coxae smooth ; hind trochanter without a transverse groove ; hind tibiae with very short spiny hairs amongst the ordinary fine pubescence visible only under high power in certain lights ; hind tarsus short, hardly more than half as long as the tibia, metatarsus about as long as the four following combined ; claws normal. Hind wing with 3 hamuli.

Gaster : rather long and slender, dorsum of the first segment smooth ; female with the ovipositor short, not extending beyond the gaster.

Affinities.—Closely allied with *H. australis*, as shown under the description of that species. Superficially a *Gasteruption*-like species.

Specimens.—Type ♂, South Australia: Adelaide (British Museum, No. 3 a. 161), (*microchela*). 1 ♂, Western Australia; 1 ♂, Swan River, Western Australia; 1 ♂, Adelaide, South Australia; 1 ♂, South Australia; 1 ♀, Ararat, Co. Ripon, Victoria.

5. *Hyptiogaster australis* (Westwood, 1835).

Foenus australis Westwood, 1835, *Proc. zool. Soc. Lond.* **3** : 51. ♂.
Foenus australis Westwood, Westwood, 1843, *Trans. ent. Soc. Lond.* **3** : 259.
Gasteruption australe (Westwood), Schletterer, 1889, *Ann. naturh.* (*Mus.*) *Hofmus Wien.* **4** : 459.
Hyptiogaster australis (Westwood), Kieffer, 1903, *Bull. Soc. ent. Fr.* **1903** : 94.
Gasteruption trianguliferum Kieffer, 1911, *Ann. Soc. ent. Fr.* **80** : 195.
Trigonofoenus triangulifer Kieffer, 1911, *Ann. Soc. ent. Fr.* **80** : 177.
Hyptiogaster australis (Westwood), Kieffer, 1912, Evaniidae, *Das Tierreich* **30** : 199.
Trigonofoenus triangulifer Kieffer, 1912, Evaniidae, *Das Tierreich* **30** : 225.
Trigonofoenus triangulifer Kieffer, Hedicke, 1939, *Hymenopterorum catalogus*, pars **11** : 42.
Hyptiogaster australis (Westwood), Hedicke, 1939, *Hymenopterorum catalogus*, pars **11** : 47.

Length : 14–16 mm.

Black with the following red: clypeus, pronotum, scutellum in part, most of the propodeum, mesopleura, ventral sides of the hind legs, mid and hind tarsi, knees of the mid-legs, and a variable amount of the ventral side of the gaster.

Head : a little broader than the thorax, prolonged and gently contracted behind (fig. 22), the occipital carina very strong; nearly smooth but vertex very finely shagreened under high power, dull; clypeus smooth, the epitomal suture well marked; malar area equal in length to the second antennal segment; frontal carina present, not very strong; distance between a posterior ocellus and the eye half that between a posterior ocellus and the occipital carina. Third antennal segment longer than the first, almost five times as long as the second, and half as long again as the fourth; terminal flagellar segments elongate.

Thorax : pronotum without processes, with V-shaped depressions, and smooth; mesonotum about as broad as long, transversely wrinkled in the male, regularly rugose in the female; pleura almost smooth; propodeum closely punctured, with a short fine median longitudinal carina above the hind coxae. Hind coxae almost smooth, hind trochanter without a transverse groove; hind tibiae with only very fine short pubescence; hind metatarsus longer than the three following segments but shorter than the four following segments together; claws normal. Hind wing with 3 hamuli.

Gaster : very finely punctured on the dorsum of the first segment; ovipositor very short, hidden, not extending beyond the end of the gaster.

Affinities.—Closely allied to *H. patellata*; these two species in their general form most nearly approach *Gasteruption*, possessing the simple form of hind tarsus found in that genus; the shape of the head and strong frontal carina together are not found in *Gasteruption*, although the outline of the head alone resembles that of Palaearctic *Gasteruption*. The long slender gaster is also reminiscent of *Gasteruption*, but the character of the wing-venation alone would be sufficient for inclusion in *Hyptiogaster*.

Specimens.—Type: ♀, Australia: (Oxford University Museum) (*australis*). Type: ♂, South Australia: (British Museum, No. 3 a. 163) (*trianguliferum*). 1 ♂, South Australia. Kieffer's type of *Gasteruption trianguliferum* (♂) in the British Museum collection has been compared with Westwood's type of *Foenus australis* (♀); these differ only in very minor points of mesonotal sculpture and very slightly in the proportions of the antennal segments; as one is male and the other female, and such small differences are frequently exhibited between the sexes in Gasteruptionidae, the writer believes the two types to belong to one species ; the venation of Kieffer's type of *G. trianguliferum* is of the *Hyptiogaster* type in which the cubitus arises from the basal vein ; bearing in mind that this was the character upon which Kieffer founded the genus *Hyptiogaster* in 1903, one wonders why he should relegate the specimen to *Gasteruption* and then *Trigonofoenus*, both of which according to his own definitions have a very different type of fore-wing venation.

6. *Hyptiogaster nitidiuscula* Turner, 1918.

Hyptiogaster nitidiuscula Turner, 1918, *Ann. Mag. nat. Hist.* (9) **1** : 411. ♂, ♀.
H. nitidiuscula Turner, Hedicke, 1939, *Hymenopterorum catalogus*, pars **11** : 49.

Length : 8–10 mm.

Red, dorsum of the thorax, propleura, and the end of the gaster somewhat fuscous.

Head : broader than the thorax, moderately elongate, and gently contracted behind the eyes ; vertex exceedingly finely shagreened, with shallow diffuse punctures, shining ; malar area shorter than the second antennal segment, frontal carina well marked ; distance from a lateral ocellus to the eye greater than half that between a lateral ocellus and the occipital collar. Third antennal segment about equal in length to the first, three and a half times as long as the second, distinctly shorter than the fourth and fifth combined (fig. 3) ; terminal flagellar segments almost quadrate.

Thorax : pronotum without processes, finely shagreened, and with diffuse shallow punctures on the dorsal third ; propleura finely shagreened ; mesonotum about as broad as long, with diffuse shallow circular punctures, the distance between the punctures far greater than their diameters ; on the anterior part of the prescutum the punctures are closer and arranged in transverse lines ; mesepisterna and metapleura leathery, mesepimera transversely striated ; propodeum finely rugose, without trace of a median longitudinal carina. Hind coxae almost smooth, but under high power seen to be very finely transversely striated ; hind trochanter without a transverse groove ; hind tibiae with very short fine spiny hairs, glabrous between these ; hind tarsi (fig. 19) symmetrical, the metatarsus about as long as the four following segments together, but much broader than these ; fifth hind tarsal segment a little shorter than the third and fourth segments combined ; metatarsus about 3·5 times as long as broad ; hind claws moderately long, but not as long as the last tarsal segment. Hind wing with 3 hamuli.

Gaster : half as long again as the rest of the body, smooth at the base ; ovipositor very short and not projecting beyond the apex of the gaster.

Affinities.—Very close to *H. inaequalis* but differs in the relative lengths of the basal antennal segments, in the diffusely punctate mesonotum, in the relative lengths and breadths of the hind tarsal segments, in the finely though diffusely punctate head, in the weaker frontal carina, shorter hind tarsal claws, and slightly smaller size ; it resembles *H. inaequalis* closely in the general form, shape of the head, coloration, proportional size and shape of the gaster and legs, and in the thoracic sculpture with the exception of that of the mesonotum.

Specimens.—Type, ♀, South-west Australia : Yallingup, 1–12.vii.1913 (*R. E. Turner*) (British Museum, No. 3 a. 143) ; 1 ♂, 10 ♀, data as for type.

7. *Hyptiogaster inaequalis* Turner, 1918.

Hyptiogaster inaequalis Turner, 1918, *Ann. Mag. nat. Hist.* (9) **1** : 410. ♀.
H. inaequalis Turner, Hedicke, 1939, *Hymenopterorum catalogus*, pars **11** : 49.

Length : 10–11 mm.

Light red, male with the head black except for a red mark by each eye, most of the mesonotum black, antennae and a line along the dorsum of the gaster black ; female with a mark on the head and part of the mesonotum black, the gaster fuscous above and the antennae fuscous-tipped.

Head : broader than the thorax, somewhat prolonged behind the eyes as in fig. 22, gently contracted posteriorly ; vertex smooth and shining ; malar area very short, not as long as the second antennal segment ; frontal carina distinct, stronger than in *H. nitidiuscula*. Distance from a posterior ocellus to the eye half that between a posterior ocellus and the hind margin of the head. Third antennal segment considerably longer than the first, nearly four times as long as the second, and just a little shorter than the fourth and fifth segments combined (fig. 4) ; terminal flagellar segments almost quadrate.

Thorax : pronotum without processes, finely shagreened, depressions closely punctured in the female, but transversely striated in the male ; mesonotum about as broad as long, rugosely punctured with transverse striation in the mesonotal furrow ; hind border of the scutum with a scooped-out shallow depression which is nearly smooth ; scutellum transversely rugose-striate ; pleura shagreened, except the epimera transversely wrinkled ; propodeum coarsely shagreened or finely punctured, without trace of a median carina. Hind coxae shagreened or minutely punctate above ; hind trochanter without a transverse groove; hind tibiae finely pitted with short sparse spiny hairs ; hind tarsus symmetrical (fig. 20), the metatarsus only twice as long as broad and equal in length to the three following segments together ; last hind tarsal segment nearly as long as the first, at most only half as broad as the metatarsus ; claws of the hind leg long and slender, equal in length to the fifth tarsal segment. Hind wing with 3 hamuli.

Gaster : not more than one and a half times as long as the head and thorax combined, more strongly clubbed terminally in the female than the male ; dorsum of the first segment smooth ; ovipositor very short, not reaching beyond the end of the gaster.

Affinities.—Close to *H. nitidiuscula* as shown in the description of that species ; these two species are quite close to the *H. australis*-group, as they have the same type of quite prolonged head, a distinct frontal carina, and the third antennal segment some 4–5 times as long as the second.

Specimens.—Type : ♀, SOUTH-WEST AUSTRALIA : Yallingup, xi.1913 (*R. E. Turner*) (British Museum, No. 3 a. 153) ; 1 ♂, 5 ♀, data as for type.

8. *Hyptiogaster szépligetii* Kieffer, 1904.

Hyptiogaster szépligetii Kieffer, 1904, *Bull. Soc. Metz* (2) **11** : 14. ♂.
Aulacofoenus szépligetii (Kieffer), Kieffer, 1911, *Ann. Soc. ent. Fr.* **80** : 177.
A. szépligetii (Kieffer), Kieffer, 1912, Evaniidae, *Das Tierreich* **30** : 193.
A. szépligetii (Kieffer), Hedicke, 1939, *Hymenopterorum catalogus*, pars **11** : 50.

Length : 12 mm.

Dark red, a characteristic anchor-shaped black mark on the mesonotum, and the dorsum of the first segment of the gaster black.

Head : very slightly wider than the thorax, contracted behind the eyes ; nearly twice as broad as long ; vertex moderately strongly shagreened ; malar area equal in length to the second antennal segment. Frontal carina absent. Distance from a posterior ocellus to the eye half that between a posterior ocellus and the occipital carina. Third antennal segment just longer than the first, three and a quarter times as long as the second, equal in length to the fourth and fifth segments together ; terminal flagellar segments quadrate.

Thorax : pronotum without processes, leathery, clothed with short pubescence, the depressions broad ; mesonotum broad and rounded, coarsely rugose, the sculpturing tending to transverse wrinkling on the median black line of the prescutum, and in the mesonotal furrows ; central part of the scutellum with broad shallow punctate striae, the lateral scutellar pockets deep and well-defining the axillae ; mesepisterna and metapleura coarsely shagreened, very pubescent, the mesepimera deep, broad, and with parallel transverse wrinkles ; propodeum finely rugose, median carina exceedingly short. Hind coxae leathery and pubescent; hind trochanter with a transverse groove; hind femora glabrous and shiny, hind tibiae finely pitted and with sparse pubescence; hind tarsi simple in the male, the metatarsus as long as the following segments combined, and the claws small; in the female the hind tarsi are characteristic, the metatarsus deeply incised, equal in length to the last segment, or to the three intermediate segments together; the latter subquadrate and equal in length to each other, the claws very large and as long as the last tarsal segment. Hind wing with 3 hamuli.

Gaster: one and a half times as long as the head and thorax together; dorsum of the first segment rugose towards the base; ovipositor short and straight, not projecting beyond the apex of the gaster.

Affinities.—A Neotropical species, near to *H. infumata* and probably closely allied to *H. deletangi*; general body form and the irregular proportions of the hind tarsal segments are features resembling the *H. inaequalis*-group.

Specimens.—7 ♀, ARGENTINA: Patquia, La Rioja Province, x.1932 (*K. J. Hayward*). Kieffer's type (♂) was described from Tucuman, Argentina; its whereabouts is unknown to the author.

9. *Hyptiogaster infumata* (Schletterer, 1889).

Gasteruption infumatum Schletterer, 1889, *Ann. naturh.* (*Mus.*) *Hofmus. Wien* **4**: 468. ♂.
Hyptiogaster infumata (Schletterer), Kieffer, 1903, *Bull. Soc. ent. Fr.* **1903**: 94.
H. infumata (Schletterer), Kieffer, 1904, *Bull. Soc. Metz* **23**: 16.
H. infumata (Schletterer), Kieffer, 1912, Evaniidae, *Das Tierreich* **30**: 195.
H. infumata (Schletterer), Hedicke, 1939, *Hymenopterorum catalogus*, pars **11**: 49.

Length: ♂, 13 mm.

Red with the following black: a mark from the upper margin of the clypeus to the anterior ocellus (remaining red by the eye margins), a mark in the ocellar triangle, the propleura, a median longitudinal line on the prescutum and the bounding furrow of the prescutum, the median furrow of the scutum, a mark on each lateral part of the scutum, and the mesepimera. Wings tinged with brownish but cannot be called dark.

Head: a little broader than the thorax, moderately strongly contracted behind the eyes, the vertex closely punctured; malar area as long as the second antennal segment; frontal carina absent. Third antennal segment three times as long as the second, fourth half as long as the third; terminal flagellar segments longer than broad.

Thorax: pronotum without processes; prescutum in the mid-line longer than the scutum and triangular, the limiting furrow broad and deep; scutum with a distinct median longitudinal furrow; prescutum and lateral parts of the scutum strongly raised and convex, strongly transversely wrinkled, coarsely punctate between the wrinkles; propodeum strongly rugose-reticulate, without trace of a median longitudinal carina. Hind coxae short and broad, transversely striate; hind trochanter with a transverse groove; hind metatarsus slightly longer than the three following segments together. Hind wing with 3 hamuli.

Specimens.—Type, ♂ (Berlin), examined by Dr. Bischoff for the author; locality: BRAZIL: S. Joao de Rey, Sao Paulo Province. Claw segments of hind tarsi missing.

10. *Hyptiogaster darwinii* (Westwood, 1841).

Foenus darwinii Westwood, 1841, *Ann. Mag. nat. Hist.* **7**: 537. ♂.
Gasteruption darwinii (Westwood), Schletterer, 1889, *Ann. naturh.* (*Mus.*) *Hofmus. Wien* **4**: 465.
Hyptiogaster darwinii (Westwood), Kieffer, 1903, *Bull. Soc. ent. Fr.* **1903**: 94.
Pseudofoenus darwinii (Westwood), Kieffer, 1912, Evaniidae, *Das Tierreich* **30**: 211.
Hyptiogaster darwinii (Westwood), Turner, 1918, *Ann. Mag. nat. Hist.* (9) **1**: 411.
H. darwinii (Westwood), Hedicke, 1939, *Hymenopterorum catalogus*, pars **11**: 48.

Length : ♂, 6 mm.

Red, fuscous on the mesonotum and scutellum, tarsi fuscous.

Head : wider than the thorax, strongly contracted behind ; vertex finely and diffusely punctured ; clypeus and inter-antennal area dull, very finely punctured ; malar area a trifle longer than the second antennal segment ; frontal carina absent ; distance between a posterior ocellus and the eye three-quarters as great as that between a posterior ocellus and the hind margin of the head. Third antennal segment a little shorter than the first, barely three times as long as the second, distinctly shorter than the fourth and fifth segments together ; terminal flagellar segments one and a half times as long as broad.

Thorax : very short and subquadrate in lateral view. Pronotum without processes, shagreened ; mesonotum about as broad as long, closely punctured and coarsely shagreened between the punctures ; scutellum with large shallow diffuse punctures and closer fine puncturation ; mesepimera rectangular and not reaching as narrow strips to the ventral side of the thorax, so that the mesepisterna and metapleura are adjacent ventral to the mesepimera ; mesopleura, metapleura, and propodeum coarsely shagreened, with a tendency to very fine striation on the latter ; propodeum without trace of a fine median longitudinal carina. Hind coxae nearly smooth ; hind trochanter without a transverse groove ; hind tibiae with very fine shallow dispersed pits and short spiny hairs ; hind tarsi asymmetrical on the first two segments (fig. 17) ; metatarsus equal in length to the last three segments, and twice as long as the fifth segment ; hind claws small. Hind wing with 3 hamuli.

Gaster : missing from the type, the only specimen in the British Museum collection, but in all probability not greatly expanded towards the apex and smooth on the dorsum of the first segment.

Affinities.—Undoubtedly a species closely related to *H. brevithorax* and *H. interrupta*, which it resembles in the asymmetric character of the hind tarsi and the formation of the mesepimeron ; the subquadrate thorax is particularly similar to that in *H. brevithorax*. The asymmetry of the hind tarsi is not so complete as in these two species as it only affects the two basal segments ; *H. darwinii* is therefore rather an intermediate species uniting the curious *H. brevithorax* and *H. interrupta* with the other species of the genus ; in addition to the asymmetry only affecting the two basal segments of the hind tarsus *H. darwinii* may be distinguished from others of the *H. brevithorax*-group by having only three hamuli on the hind wing, and by the small size.

Specimens.—Type : ♂, AUSTRALIA (*C. Darwin*) (British Museum, No. 3 a. 142).

11. *Hyptiogaster brevithorax* (Kieffer, 1911).

Hemifoenus brevithorax Kieffer, 1911, *Ann. Soc. ent. Fr.* **80** : 182. ♀.
H. brevithorax Kieffer, Kieffer, 1912, Evaniidae, *Das Tierreich* **30** : 192.
H. brevithorax Kieffer, Hedicke, 1939, *Hymenopterorum catalogus*, pars **11** : 50.

Length : ♀, 10·5 mm.

Red with the thorax mainly fuscous.

Head : slightly broader than the thorax, contracted behind the eyes ; vertex with a very short transverse furrow immediately behind the ocelli, moderately and closely punctured ; clypeus and inter-antennal area glabrous, exceedingly minutely punctured ; malar area at least one and a half times as long as the second antennal segment ; frontal carina absent. Ocelli small, distance between a posterior ocellus and the eye three-quarters of that between a posterior ocellus and the hind margin of the head. Third antennal segment about equal in length to the first, three times as long as the second, shorter than the fourth and fifth segments combined ; terminal flagellar segments about twice as long as broa

Thorax : pronotum without processes, finely shagreened ; propleura finely shagreene rather broadened when viewed from above ; mesonotum about as broad as long, furrows deep, and with shallow diffuse puncturation, shagreened between the punctures ; scutellum finely punctured and with two unbroken longitudinal scutellar furrows ; pleura shagreened ; propodeum finely transversely striated, without a short fine median carina. Form of the thorax when viewed laterally very deep, nearly as high as long, and subquadrate. Hind coxae smooth ; hind trochanter without a transverse groove ; femora short and thick, tibiae only very slightly longer than the femora ; hind tarsi (fig. 15) asymmetrical on all segments except the last ; each of the first four segments with a strongly developed tooth on the outer side ; metatarsus shorter than the three following segments combined, fifth segment about equal in length to the second ; claws normal. Hind wing with 4 hamuli.

Gaster : one a half times as long as the head and thorax together, with fine rugulose sculpturing on the dorsum of the first segment ; strongly widened towards the end when viewed laterally ; ovipositor short, slightly curved, hidden, not emerging beyond the gaster.

Male unknown.

Affinities.—A very characteristic species very closely allied to *H. interrupta* sp. n., but differing in the subquadrate thorax and the complete scutellar furrows. Kieffer separated this species from other *Hyptiogaster* on the square thorax, but this is found in several other species, e.g., *H. minima* and *H. darwinii*. The latter species has somewhat asymmetrical hind tarsi and appears to be fairly close to *H. brevithorax*. Kieffer evidently considered the asymmetrical hind tarsi a supporting character for his genus *Hemifoenus*, but since his Evaniidae in *Das Tierreich* (1912) several species exhibiting this feature to a greater or lesser extent have been noticed, *H. darwinii* especially being an intermediate between the fully asymmetrical tarsus of *H. brevithorax* and the symmetrical tarsus of most other *Hyptiogaster*.

Specimens.—Type : ♀, AUSTRALIA : Melbourne, Victoria, 1907 (*R. E. Turner*) (British Museum, No. 3 a. 141).

12. **Hyptiogaster interrupta** sp. n.

Length : ♀, 10 mm.

Entirely red.

Head : a little wider than the thorax, and contracted behind the eyes ; shining with shallow diffuse punctures ; clypeus and inter-antennal area finely shagreened with scarcely visible pubescence ; malar area one and a half times as long as the second antennal segment ; frontal carina absent. Ocelli close together, connected by narrow furrows ; distance from the eye to a posterior ocellus three quarters as great as that between a posterior ocellus and the occipital carina. Third antennal segment longer than the first, three times as long as the second, and two-thirds as long as the fourth and fifth segments together ; terminal flagellar segments one and a half times as long as broad.

Thorax : pronotum without processes, finely shagreened, the pronotal depressions broad and shallow with short thick pubescence ; mesonotum about as broad as long, with small shallow diffuse punctures, very finely shagreened between the punctures ; mesonotal furrow well marked but not deep, parapsidal furrows distinct ; central part of the scutellum almost smooth, but the lateral longitudinal scutellar grooves interrupted ; mesopleura shagreened, the epimera well defined as rectangular sclerites not reaching to the ventral side of the thorax ; metapleura shagreened, differentiated into upper and lower parts separated by the deep pits of the pleural apophyses ; propodeum very coarsely shagreened, the shagreening running in fine transverse striae ; median longitudinal carina on the propodeum above the hind coxae. Form of the thorax when viewed laterally quite clearly elongate and not subquadrate. Hind coxae smooth, hind trochanter without a transverse groove ; hind femur short and broad, the tibia distinctly longer than the femur ; hind tarsi with the extreme asymmetry and relative lengths of the segments as in *H. brevithorax* (fig. 15). Hind wing with 4 hamuli.

Gaster : barely one and a half times as long as the rest of the body, smooth and shining above right to the base ; strongly widened when viewed laterally ; ovipositor short, hidden, not protruding beyond the apex of the gaster.

Affinities.—Only very close to *H. brevithorax* but differs in the shape of the alitrunk, in the broken scutellar grooves, the proportionately longer hind tibia, the carinate propodeum, and in other minor differences ; the curious asymmetrical hind tarsi are identical with those of *H. brevithorax.*

Type : ♀, TASMANIA : Mt. Wellington, i.1913 (*R. E. Turner*). In the British Museum.

13. *Hyptiogaster plicata* (Schletterer, 1889).

Gasteruption plicatum Schletterer 1889. *Ann. naturh.* (*Mus.*) *Hofmus. Wien* **4** : 466. ♂.
Hyptiogaster plicata (Schletterer), Kieffer, 1903, *Bull. Soc. ent. Fr.* **1903** : 94
Eufoenus plicatus (Schletterer), Szépligeti, 1903, *Ann. hist.-nat. Mus. hung.* **1** : 365.
Hyptiogaster plicata (Schletterer), Kieffer, 1912, Evaniidae, *Das Tierreich* **30** : 199.
H. plicata (Schletterer), Hedicke, 1939, *Hymenopterorum catalogus*, pars **11** : 49.

Length : ♂, 15·5 mm.

Black, with red on the lower border of the clypeus, round the inner edge of each eye, on the pronotum (centre parts of the lateral lobes blackish), on the mesoscutum except for a large black middle mark which extends also on to the prescutum ; the scutellum red except the axillae, and the mesopleura red ; metapleura and propodeum black ; middle and hind coxae largely red, hind femora largely red but darkened at the bases and apices ; second to fifth tergites of the gaster somewhat reddened ; hind tarsi white, except the bases of the metatarsi.

Head : fairly strongly contracted behind the eyes ; very finely sculptured with radial sculpture round the ocelli, and microscopic furrowing behind the ocelli ; temples shining punctate ; occipital carina very narrow ; malar area longer than the second antennal segment ; frontal carina absent. Third antennal segment three and a half times as long as the second, fourth perceptibly shorter than the third ; terminal flagellar segments missing from the type.

Thorax : pronotum without processes ; mesonotum very convex, strongly transversely wrinkled on the prescutum and lateral parts of the scutum, punctured between the wrinkles ; median part of the scutum very strongly rugose ; scutellum convex, strongly and irregularly rugose ; propodeum irregularly rugose, with a short fine median carina above the posterior coxae. Hind coxae shining above, not striated ; hind trochanter without a transverse groove ; hind tarsi symmetrical, metatarsus 3·3 times as long as broad, and slightly lobed at the end, thus giving a very slight asymmetry ; metatarsus longer than the three following segments but shorter than the four following segments together ; second segment equal in length to the third and fourth together ; claws small. Hind wing with 3 hamuli.

Specimens.—Type, ♂ (Berlin), examined by Dr. Bischoff for the author ; locality, AUSTRALIA : Sydney, New South Wales.

14. *Hyptiogaster pilosa* Kieffer, 1911.

Hyptiogaster pilosa Kieffer, 1911, *Ann. Soc. ent. Fr.* **80** : 180. ♂
H. pilosa Kieffer, Kieffer, 1912, Evaniidae, *Das Tierreich* **30** : 200.
H. pilosa Kieffer, Hedicke, 1939, *Hymenopterorum catalogus*, pars **11** : 49.

Length : ♂, 7–11 mm.

Head and thorax black, gaster black at the base and apex, the middle segments reddish-fuscous ; mandible, scape of the antenna, and the legs reddish-fuscous ; red mark and white pubescence on the end of each segment of the gaster except the last two ; knees yellowish.

Head : broader than the thorax, nearly twice as wide as long, with the hind angles well marked (fig. 23) ; frontal carina absent, malar area equal in length to the second antennal segment ; head very shining but very finely punctured. Distance from a posterior ocellus to the eye almost as great as that between a posterior ocellus and the occipital carina ; first four segments of the antennae with outstanding pubescence, third segment equal in length to the first, four times as long as the second, and equal in length to the fourth and fifth segments combined ; terminal flagellar segments as broad as long.

Thorax : pronotum without processes, finely shagreened, with long pubescence, the depressions broad ; mesonotum about as broad as long, the furrows deep, and with strong distinctive punctures, the punctures a little broader than the interspaces ; scutellum rugosely punctured ; mesopleura with long pubescence, coarsely shagreened ; propodeum finely rugulose, without trace of a median carina. Hind coxae nearly smooth, but with fine striations visible under high power ; hind trochanter without a transverse groove ; hind femora sparsely pubescent beneath, tibiae with long outstanding pubescence ; hind tarsi symmetrical, very hairy, the metatarsus a little shorter than the four following segments combined, but much broader than these ; claws normal. Hind wing with 4 hamuli.

Gaster : each segment with long outstanding pubescence. Female unknown but would undoubtedly have the hidden ovipositor.

Affinities.—An unspecialised member of the genus, having the simple hind tarsi and lacking a frontal carina as in the *H. ritae* and *H. floricola* type : the well-marked hind angles of the head and the strongly pubescent gaster distinguish the species from all other *Hyptiogaster.*

Specimens.—Type : ♂, AUSTRALIA : Kuranda, Queensland, xi.1904 (*F. P. Dodd*) (British Museum, No. 3 a. 158). 1 ♂, AUSTRALIA : Mackay, Queensland, 1910 (*R. E. Turner*) ; 1 ♂ (genitalia missing), F. Smith collection.

15. *Hyptiogaster extranea* Turner, 1918.

Hyptiogaster extranea Turner, 1918, *Trans. ent. Soc. Lond.* **51** : 342. ♂.
Hemifoenus extraneus (Turner), Brues, 1922, *Psyche, Camb., Mass.* **29** : 11.
Hemifoenus extraneus (Turner), Hedicke, 1939, *Hymenopterorum catalogus*, pars **11** : 50.

Length : ♂, 7 mm.

Light red, the outer sides of the hind femora and tibiae dark, gaster blackish with a red mark on the end of each segment.

Head : broader than the thorax, strongly contracted behind the eyes ; vertex finely shagreened, clypeus minutely punctured ; malar area as short as the second antennal segment ; frontal carina absent. Distance from a posterior ocellus to the eye half that between a posterior ocellus and the occipital carina. Third antennal segment equal in length to the first, four times as long as the second, one a half times as long as the fourth ; terminal flagellar segments about twice as long as broad.

Thorax : subquadrate seen from the side. Pronotum without processes, the anterior and dorsal sectors coarsely shagreened, the posterior sector with regular parallel carinae ; mesonotum with deep furrows, the prescutum very strongly raised and rounded ; each side of the scutum also strongly convex ; parapsidal furrows not evident ; both prescutum and scutum with regular curved parallel ridges ; the pointed apex of the prescutum nearly reaching to the scutellum ; scutellum strongly raised with well-developed lateral carinae, the area between the carinae crossed by reticulate ridges and furrows ; mesepisterna coarsely shagreened, mesepimera smooth and shining except for three transverse ridges at the dorsal end ; metapleura smooth and shining ; propodeum rugose with a number of transverse carinae, and two parallel longitudinal carinae extending down from the insertion of the gaster for about one-fifth of the length of the posterior declivity of the propodeum; also a short median longitudinal carina above the hind coxae. Hind coxae finely transversely striated; hind trochanter without a transverse groove; hind femora smooth and shining, hind tibiae clothed with very short close pubescence and long outstanding pubescence; hind tarsi symmetrical, the metatarsi a little broader than the other segments, longer than the three following but shorter than the four following together; fifth segment as long as the second; claws normal. Hind wing with three hamuli.

Gaster: slender, the dorsum of the first segment smooth and shining; female unknown, but would have probably the hidden ovipositor.

Affinities.—A rather isolated species, as might be expected from its apparent confinement to certain islands of the Fiji group; the arched mesonotum with its regular parallel shining carinae is quite characteristic and not found in other *Hyptiogaster*; Turner (1918) suggests that the species is close to *H. darwinii*, but the simple symmetrical tarsi, the humped mesonotum and carinate scutellum make this rather unlikely, although the subquadrate form of the thorax is a resemblance to the *H. brevithorax*-group. Brues (1922) obtained further specimens of *H. extranea* from Fiji, and it was apparently this feature of the short, deep thorax which led him to include the species with Kieffer's *H. brevithorax* under *Hemifoenus* Kieffer; there can be little relationship between *H. brevithorax* and *H. extranea* when one takes into consideration the nature of the notal region of the thorax and the asymmetric character of the hind tarsi of the former species; further, this character of the quadrate thorax is to be found in *H. minima* which is certainly in no way a close relative of *H. brevithorax.* As pointed out in the introductory part of this paper, *Hemifoenus* Kieffer has been suppressed.

Specimens.—Type: ♂, Fiji Islands: Cuvu, 17.vi.1915 (*R. Veitch*) (British Museum, No. 3 a. 156). Brues (1922) also records the following: 5 ♂, Nadarivatu, Fiji; and 1 ♂, Navai, Fiji; from the collection of W. M. Mann.

16. *Hyptiogaster antennalis* (Schletterer, 1889).

Gasteruption antennale Schletterer, 1889, *Ann. naturh.* (*Mus.*) *Hofmus. Wien* **4**: 464. ♂.
Hyptiogaster antennalis (Schletterer), Kieffer, 1903, *Bull. Soc. ent. Fr.* **1903**: 94.
Eufoenus antennalis (Schletterer), Szépligeti, 1903, *Ann. hist.-nat. Mus. hung.* **1**: 365.
Hyptiogaster antennalis (Schletterer), Kieffer, 1912, Evaniidae, *Das Tierreich* **30**: 202.
H. antennalis (Schletterer), Hedicke, 1939, *Hymenopterorum catalogus,* pars **11**: 47.

Length: ♂, 9–10 mm.

Black with a variable amount of red; mandibles red, the pronotum in part, the bounding furrow of the prescutum, the side margins and mid-line of the scutum, the scutellum (except a median black fleck), the meso- and metapleura (except the upper ends of the mesepimera), the tegulae, the coxae and legs (except the front legs brownish) red; gaster entirely black.

Head: short and broad, the hind angles almost as well-marked as in *H. pilosa*; strongly rugose, without striation; malar area as long as the second antennal segment; frontal carina absent; third antennal segment three times as long as the second, fourth half as long as the third. Terminal flagellar segments quadrate.

Thorax: pronotum without teeth; mesonotum coarsely rugose; propodeum finely shagreened, and with a short fine median carina above the hind coxae. Hind coxae distinctly transversely striated above, finely punctured on the lateral and ventral sides, indistinctly punctured in the striated areas; hind trochanter without a transverse furrow; hind tarsi symmetrical, metatarsus three times as long as broad, a little longer than the three succeeding segments, but much shorter than the four following segments together; fifth tarsal segment half as long as the first, equal in length to the third and fourth together; claws small. Hind wing with 3 hamuli.

Gaster : with fine silky pubescence on the postero-lateral border of the second and succeeding segments.

Specimens.—Type : ♂ (Berlin), examined by Dr. Bischoff for the author; locality : AUSTRALIA.

17. **Hyptiogaster microcephala** sp. n.

Length : ♀, 8 mm.

Predominantly black, side borders of the prescutum red, pronotum and scutellum largely red, a red mark across the mesopleura, propodeum red, underside of the hind legs red, and a mark on each segment of the gaster yellowish.

Head : broader than the thorax, and about twice as wide as long (fig. 24); hind margin gently incurved with a narrow occipital carina, eyes prominent; vertex coarsely shagreened with strong radiating striae round each ocellus; clypeus finely and closely punctured, the epistomal suture very distinct; malar area equal in length to the second antennal segment; frontal carina absent. Distance between the posterior ocelli very slightly greater than that between a posterior ocellus and the eye (fig. 24); distance from a posterior ocellus to the eye about three-quarters as great as that between a posterior ocellus and the occipital carina. Third antennal segment longer than the first, three times as long as the second, and a little more than one and a half times as long as the fourth; terminal flagellar segments about one and a half times as long as broad.

Thorax : only slightly elongate viewed from the side; pronotum without processes, finely shagreened, the pronotal depressions shallow; mesonotum about as broad as long, coarsely rugose-reticulate with a tendency towards transverse carinae, the prescutal sutures distinct; anterior border of the prescutum nearly straight (fig. 24), the angles well marked, the length of the prescutum about as great as its width; scutellum strongly rugose-reticulate; mesepisterma coarsely shagreened, mesepimera irregularly transversely striated; metapleura shagreened; propodeum strongly shagreened and without trace of a fine median carina above the hind coxae. Hind coxae finely shagreened, hind trochanter without a transverse groove; hind tarsi symmetrical, the metatarsus as long as the three following segments together; claws small. Anterior discoidal cell of the fore-wing three-cornered, hind wing with 3 hamuli.

Gaster : almost twice as long as the head and thorax combined, not greatly expanded towards the end when viewed laterally, dorsum of the first segment exceedingly finely shagreened; very short, hidden, ovipositor not reaching beyond the apex of the gaster.

Affinities.—The species is closely allied to *H. ritae* but differs as follows : in the wider spaced posterior ocelli, the broader and rather more deeply incurved posterior margin of the head (cf. figs. 24 and 25); in the radiating sculpture around the ocelli, and the thicker antennae with relatively shorter terminal flagellar segments; in the straight anterior edge to the prescutum, with well-marked corners, and the length of the prescutum about as great as the width (cf. figs. 24 and 25); in the more finely sculptured propodeum without a trace of a short fine median longitudinal carina above the hind coxae, and the absence of transverse striation on the hind coxae; in the three-cornered anterior discoidal cell (1M) of the fore wing, and the cubitus arising from almost exactly the middle of the basal vein; and also in minor differences of body sculpture; the legs are of rather different proportions, the hind femora and tibiae shorter and stouter, about 4·5 times as long as broad, compared with about 6 times as long as broad in *H. ritae*; hind metatarsus about 3 times as long as broad, about 5 times as long as broad in *H. ritae*. *H. microcephala* is from Australia, while *H. ritae* has only been taken from three islands of the New Hebrides group.

Type.—♀, WESTERN AUSTRALIA: Dongarra, 245 miles north of Perth, 20–25.ix.1935 (*R. E. Turner*). In the British Museum (Natural History).

18. *Hyptiogaster ritae* Cheesman, 1936.

Hyptiogaster ritae Cheesman, 1936, *Trans. R. ent. Soc. Lond.* **85**: 176. ♂, ♀.
H. ritae Cheesman, Hedicke, 1939, *Hymenopterorum catalogus* pars **11**: 49.

Length: 8–10 mm.

Dark reddish-fuscous, mesonotum, dorsal side of hind femur and tibiae and the flagellum of the antenna black; gaster black on the base of each segment.

Head: broader than the thorax, contracted behind, occipital carina narrow and only very slightly incurved (fig. 25); very nearly twice as broad as long, eyes very prominent; vertex with scattered punctures, sometimes transversely striate behind the ocelli, but never with radiating striae round the ocelli; clypeus indistinctly punctured; malar area short, about as long as the second antennal segment; frontal carina absent. Distance between the posterior ocelli a little smaller than that between a posterior ocellus and the eye (fig. 25); distance from a posterior ocellus to the eye a little over two-thirds of that between a posterior ocellus and the occipital carina. Third antennal segment as long as the first, four times as long as the second, and one and a half times as long as the fourth; terminal flagellar segments about twice as long as broad.

Thorax: pronotum without processes, coarsely shagreened, the depressions shallow and broad, longitudinal striations on the posterior sector; mesonotum a trifle longer than broad, densely and coarsely reticulate; prescutum evenly and gently curved along the anterior border (fig. 25), the corners very rounded, distinctly broader than long; scutellum irregularly transversely reticulate; mesepisterna divided into upper and lower parts by a line of large punctures, the upper part coarsely shagreened, lower part finely rugose; mesepimera broad with fairly regular transverse wrinkles, shining; metapleura with shallow rugose reticulations, coarsely shagreened near the metanotum; propodeum rugose, with a transverse carina slightly nearer to the coxal insertions than to the insertion of the gaster; more coarsely rugose between the carina and the hind coxae than in the upper sector; lower sector with a short fine median longitudinal carina. Hind coxae finely transversely striate; hind trochanter without a transverse groove; hind femora and tibiae long and narrow, tibiae with long thick pubescence; hind tarsus quite symmetrical, the metatarsus somewhat thicker than the succeeding segments, and about five times as long as broad; metatarsus longer than the next three segments but shorter than the succeeding four segments together; claws normal. Hind wing with 3 hamuli; anterior discoidal cell with four corners.

Gaster: nearly twice as long as the rest of the body, not greatly expanded towards the end, dorsum of the first segment smooth; ovipositor very short, not protruding beyond the apex of the gaster.

Affinities.—Very closely allied to the new species *H. microcephala* from which it can be distinguished by the differences listed under that species, but it also shows intermediate features between the *H. australis*-group and the rather unspecialised species *H. floricola* and *H. minima*.

Specimens.—The species is represented by a number of specimens taken by Miss Cheesman on three islands of the New Hebrides.

Type.—♂, NEW HEBRIDES: Aneityum, x.1930 (*L. E. Cheesman*) (British Museum, No. 3 a. 157); paratypes: 3 ♂, 2 ♀, NEW HEBRIDES: Aneityum, x.1930 ; 2 ♂, 2 ♀, New Hebrides : Ounua, Malekula, 2.iv.1929 ; 1 ♀, New Hebrides : Tanna, x.1930.

19. *Hyptiogaster floricola* Turner, 1918.

Hyptiogaster floricola Turner, 1918, *Ann. Mag. nat. Hist.* (9) **1** : 412. ♂, ♀.
H. floricola Turner, Hedicke, 1939, *Hymenopterorum catalogus*, pars **11** : 48.

Length : 5–6 mm.

Largely black ; head shining black, pleura, gaster, and legs reddish-fuscous ; pronotum, propodeum, mesepimera, mandibles and ovipositor red ; knees yellow in the male.

Head : much broader than the thorax, strongly contracted behind the eyes ; vertex smooth and very shining, face with fine close puncturation ; lateral borders of the clypeus marked by broad deep foveae which are sometimes transversely striated ; epistomal suture between the clypeus and inter-antennal area missing ; malar area only as long as the second antennal segment ; frontal carina absent ; distance between a posterior ocellus and the eye three-quarters as great as that between a posterior ocellus and the occipital carina. Third antennal segment longer than the first, three and a half times as long as the second, very nearly as long as the fourth and fifth segments together ; terminal flagellar segments almost quadrate.

Thorax : pronotum rugulose, without processes, transversely wrinkled in the depressions ; mesonotum as long as broad, rounded at the anterior angles, furrows deep, coarsely rugose, somewhat transversely rugose-striate on the prescutum ; scutellum rugose, the axillae somewhat pointed and projecting ; upper parts of the mesepisterna finely punctate, lower parts pubescent and finely rugulose ; mesepimera transversely wrinkled and extending to the ventral side of the thorax ; metapleura smooth medially and transversely striate dorsally and ventrally ; propodeum rugulose with a fine transverse carina nearer to the hind coxae than to the insertion of the gaster, median longitudinal carina not developed. Hind coxae very finely transversely striated ; hind trochanter without a transverse groove ; hind femora glabrous, hind tibiae minutely punctate ; hind tarsi simple and symmetrical (fig. 18), the metatarsus as long as the remaining segments together, but broader than these ; hind claws small. Hind wing with 3 hamuli.

Gaster : only a very little longer than the head and thorax combined, strongly expanded towards the end especially in the female, dorsum of the first segment smooth and shining ; ovipositor short, somewhat curved, not projected beyond the end of the gaster.

Affinities.—Very closely allied to *H. minima* from which it can be best distinguished by the key characters ; it is also quite close to *H. ritae* ; probably the least specialised species of *Hyptiogaster*.

Specimens.—Type : ♀, South-west Australia : Kalamunda, 9–28.ii.1914 (*R. E. Turner*) (British Museum, No. 3 a. 152) ; cotype : ♂, data as for type ; paratypes : 3 ♂, 20 ♀, data as for type.

Habit.—Taken on the blossoms of *Eucalyptus calophylla* R. Br.

20. *Hyptiogaster minima* Turner, 1918.

Hyptiogaster minima Turner, 1918, *Ann. Mag. nat. Hist.* (9) **1** : 412. ♀.
H. minima Turner, Hedicke, 1939, *Hymenopterorum catalogus*, pars **11** : 49.

Length : ♀, 4 mm.

Mainly black, clypeal margin, mesonotal furrows, pleura, propodeum, and legs somewhat ferruginous ; gaster with a narrow white border on the end of each segment, ovipositor red ; mandibles and a mark round each eye red.

Head : broader than the thorax, strongly contracted behind the eyes ; vertex finely and closely punctured ; front of the face glabrous, anterior tentorial pits and epistomal suture well marked; malar area one and a half times as long as the second antennal segment; frontal carina absent. Distance from a posterior ocellus to the eye two-thirds of that between a posterior ocellus and the occipital carina. Third antennal segment a little shorter than the first, two and a half times as long as the second, and one-third as long again as the fourth; terminal flagellar segments one and a half times as long as broad.

Thorax: subquadrate when viewed from the side. Pronotum without processes, coarsely shagreened, depressions shallow; mesonotum very short, broader than long, moderately and closely punctured; the prescutal sutures well marked, the area between them depressed and traversed by striae; mesonotal furrows with large punctures separated by ridges; scutellum finely punctured with lateral longitudinal furrows; mesopleura and metapleura finely and closely punctured, the epimera rectangular and not reaching to the ventral side of the thorax, the condition shown also in the *H. brevithorax*-group. Propodeum finely transversely rugulose, without a median carina above the hind coxae. Hind coxae very nearly smooth, shining; hind trochanter without a transverse groove; femora with long sparse outstanding pubescence; hind tibiae with long sparse hairs among the ordinary short pubescence; hind tarsi symmetrical, metatarsus as long as the four following segments combined, and not very broadened; claws small. Hind wing with 3 hamuli.

Gaster: not more than one and a quarter times as long as the rest of the body, dorsum of the first segment exceedingly finely sculptured; ovipositor short, slightly curved, not extending beyond the apex of the gaster.

Male unknown.

Affinities.—Close to *H. floricola*, and showing also the unspecialised features as in *H. ritae*. In character of the mesepimera *H. minima* resembles the *H. brevithorax*-group, but it is unlikely that the relationship with these is very close; longer bristles are developed on the outer sides of the ends of the hind tarsal segments than on the inner sides, and it is just possible that this represents the very first stage in the development of tarsal asymmetry.

Specimens.—Type: ♀, S. TASMANIA: Mt. Wellington, 15.i.1913 (*R. E. Turner*); taken at 2300 feet (British Museum, No. 3 a. 144).

8. DESCRIPTIONS OF THREE SPECIES OF *Hytiogaster* WHICH THE AUTHOR HAS BEEN UNABLE TO EXAMINE OR HAVE EXAMINED FOR HIM, AND WHICH CANNOT THEREFORE BE INCLUDED IN THE KEY TO THE GENUS; THESE DESCRIPTIONS ARE TRANSLATED FROM THE ORIGINALS IN KIEFFER, 1907, AND SCHLETTERER, 1893.

Hyptiogaster deletangi (Schletterer, 1893).

Gasteruption deletangi Schletterer, 1893, *Ent. Nachr.* **19**: 166. Dalla Torre, 1902, *Cat. Hym.* **3**: 1066. Schulz, 1906, *Spolia. Hym.*: 133.

Hyptiogaster deletangi (Schletterer), Kieffer, 1904, *Bull. Soc. Metz* **23**: 16. Kieffer, 1912, Evaniidae, *Das Tierreich* **30**: 195. Hedicke 1939, *Hymenopterorum catalogus*, pars **11**: 48.

Length: ♀, 10 mm.

Red. Head behind the ocelli shining and sparsely punctured, strongly punctured between the antennae, clypeus shining; frontal carina absent, malar area short. Mandibles elongate. Head broader than the thorax and abbreviated behind the eyes; third antennal segment longer than the two following but shorter than the three following together. Pronotum without processes; mesonotum strongly convex, shining and with moderately dense punctures; mesonotal suture deep. Propodeum shining but conspicuously punctured. Hind coxae short and thick, smooth and shining; hind metatarsus shorter than the following segments combined; hind claws large. Gaster strongly clavate, ovipositor very short.

Locality.—Neotropical; Argentina, Parana. Type: Vienna ?. (From Schletterer's description it seems likely that this is closely related to the other Neotropical species, *H. infumata* and *H. szépligetii.*)

Hyptiogaster crassitarsis Kieffer, 1907.

Hyptiogaster crassitarsis Kieffer, 1907, *Berl. ent. Z.* **51** : 271. Kieffer, 1912, Evaniidae, *Das Tierreich* **30** : 198. Hedicke, 1939, *Hymenopterorum catalogus*, pars **11** : 48.

Length : ♂, 10 mm.

Black, borders and furrows of the mesonotum, sides of the scutellum, a mark on the mesopleura and the middle of the propodeum reddish-brown; undersides of the hind coxae and femora and the bases of the tibiae red-brown. Head rounded, shining, finely striated. Distance between the posterior ocelli equal to that between a posterior ocellus and the eye; frontal carina present, malar area short. First antennal segment equal to the third, second as broad as long, third three times as long as the second. Pronotum without processes; mesonotum strongly and irregularly wrinkled; prescutum triangular and bounded by a deep furrow; scutellum strongly rugose; propodeum finely rugose with a median carina. Hind coxae finely transversely striated, all tibiae and tarsi with thick outstanding pubescence; hind metatarsus thick, scarcely as long as the three following segments together, second segment of the hind tarsus bilobed, not longer than broad; hind claws narrow, half as long as the fifth tarsal segment. Wing veins and pterostigma brown. Gaster with the hind part of each tergite red-brown.

Locality.—South-west Australia: Subiaco. Taken in September. Type ?.

Hyptiogaster flavinervis Kieffer, 1907.

Hyptiogaster flavinervis Kieffer, 1907, *Berl. ent. Z.* **51** : 272. Kieffer, 1912, Evaniidae, *Das Tierreich*, **30** : 199. Hedicke, 1939, *Hymenopterorum catalogus*, pars **11** : 48.

Length : ♂, 9 mm.

Reddish-yellow, head black except for the border of the clypeus, the mandibles, a line behind the ocelli and the malar area; gaster brown, yellowish on the end of each tergite. Head somewhat longer than broad, smooth, finely punctured with large scattered punctures, finely striated behind the ocelli; an impressed line present from the anterior ocellus to between the antennae, and another from the scape of each antenna to the clypeus; malar area a little longer than the second antennal segment, frontal carina absent. Antenna black except for the base of the scape; first antennal segment a little longer than the third, second not longer than broad, third somewhat longer than the fourth, the latter twice as long as broad. Thorax black above except for the hind margin of the mesonotum and the anterior border of the scutellum; each side of the propodeum with a blackish-brown mark; pronotum without processes; mesonotum and scutellum strongly transversely striated; prescutum triangular; propodeum very finely transversely striated; pleura smooth with silvery pubescence; hind coxae smooth, hind tibiae with short thick outstanding hair; hind metatarsus not very thickened and as long as the three following segments together; hind claws half as long as the fifth tarsal segment. Wings with veins and pterostigma yellowish, hind wing with 4 hamuli.

Locality.—New South Wales. Type ?.

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A STUDY OF THE TRAMINI (HOMOPTERA—APHIDIDAE).

By V. F. Eastop, M.Sc., F.R.E.S.

(*Department of Zoology, Cambridge University.*)

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(With 1 Plate and 1 Text-figure.)

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Introduction.

The Tramini is a little worked natural group of root-feeding aphids which is characterised by the second tarsal segment of the hind leg being greatly elongate. As the apterae are large, white, and have the habit, when disturbed, of rapidly vibrating the elongate hind tarsi, and feed almost exclusively on the roots of Compositae, the group is readily recognised in the field. The colonies are almost invariably accompanied by ants and some species cannot be kept without them.

The two major systematic works on the Tramini are those of Del Guercio (1909) and Mordwilko (1935). Börner (1952) has listed the European species together with their host plants.

The first known mention of this group was in 1837 when von Heyden erected the genus *Trama* for his new species *troglodytes*. The first records of *Protrama* and *Neotrama* were in 1843, when Kaltenbach described *Trama radicis*, which is a mixture of species belonging to the two genera. Del Guercio was the first to recognise that *Neotrama* were not the larvae of *Protrama* when, in 1909, he described *Trama caudata* and *T. horvathi*, which are here placed in *Neotrama*. *Trama* has been recognised as a valid genus by most authors since its erection in 1837, an exception being Ferrari, who, in 1872, described a *Protrama* and a *Neotrama* as *Lachnus longitarsus*. Most authors up to the beginning of the twentieth century placed *Trama* near *Paracletus* and *Forda*, but Buckton (1881) placed *Trama* in the Lachninae, which is now its generally accepted position. Baker (1920) erected the Tramina as a sub-tribe of the tribe Lachnini for *Trama* and his two newly described genera, *Protrama* and *Neotrama*. Oestlund (1922) used a tribe Tramini as a division of his supertribe Lachnea. Börner (1952) regards the group as a sub-family, the Traminae, of his family Lachnidae. In this paper the Tramini is regarded as a tribe of the sub-family Lachninae.

Del Guercio (1899) gives an account of the behaviour of the sexuales of a *Protrama* (as *Trama troglodytes*). Although this reference is given in his 1909 monograph of the group, he neither describes nor figures the sexuales. It is stated that both the males and oviparae are apterous. Mordwilko (1935) states that he may have reared one alate male of a *Protrama* (as *Trama radicis*); this is not described or figured and no further references to the sexuales of the Tramini are known. Sexuales of this group have not been found in the field by the author nor reared in the laboratory by subjecting material to changing conditions of light and temperature.

CHARACTERS OF THE TRIBE TRAMINI.

Macroscopic Morphology.

Medium to large-sized aphids, the adults varying from two and a half to four millimetres long. Alatae have head and thorax black or dark brown, and the paler abdomen crossed by segmentally arranged black bars that reach almost to the pigmented lateral sclerites. True apterae have no pigmentation and are white or whitish, but, as most of the specimens examined were to some extent alatiform, they had some of the pigmentation of the alatae. Apterae of *Trama* and *Neotrama* (the Tramina) usually have head and thorax only slightly pigmented, even when the structure of the head and antennae is distinctly alatiform. The first alatiform character to appear in *Protrama* is the pigmentation, and this is frequently present when the head and antennae are only slightly alatiform structurally. As true apterae are rare in the Tramini most specimens of *Protrama* seen are apterous but have the pigmentation of alatae.

Microscopic Morphology.

Head, thorax, abdomen and appendages furnished with numerous fine pointed hairs about 65 μ long. (*Trama antennata* is said to have hairs of two different lengths on the legs. This species has not been seen by the author or recorded by anyone else since its original description from Turkestan.) Head distinctly divided in alatae and in alatiform apterae, but the suture is faint or absent in true apterae, which are very rare. Eyes of alatae large and of many facets, of alatiform apterae variable and of true apterae, a small compound eye in *Protrama* and only a triommatidion, or with a few more facets, in *Trama*. Antennae six segmented in adults and about half length of body, and with a primary rhinarium at apex of segment 5 and on segment 6. Antennae of first instar larvae five segmented. Secondary rhinaria absent in true apterae but present and round in alatae and alatiform apterae. Primary rhinaria not or only very faintly ciliated. Processus terminalis very little developed, and never as long as base of sixth antennal segment and often very much shorter. Processus terminalis bears 5 to 9 short apical hairs and 0 to 16 normal antennal hairs. Rostrum well developed, being as long as the body in small larvae and reaching to between third and fifth abdominal segments of adults.

Radius of fore wing slightly bent and placed near apex of wing. Media of fore wing faint and usually once or twice branched, but sometimes simple in brachypterae. Hind wings with both media and cubitus present. Legs long, tarsi and second pairs of legs normal, those of hind legs with the first segment much reduced and the second greatly elongate. Hind tarsus/hind tibia ratio varies from 0·5 to 0·95. In any particular species this ratio higher in apterae than in alatae. Thus in *Protrama ranunculi* the slightly alatiform apterae have the ratio varying from 0·55 to 0·63, the very alatiform apterae from 0·50 to 0·60 and the true alatae from 0·50 to 0·57. Alatiform apterae and brachypterous intermediates very common in the Tramini and usually much more abundant than either true apterae or alatae. True apterae of some species and alatae of others have never been found or reared in the laboratory. A pair of claws present at apex of all second tarsal segments. Empodial hairs short, only rarely more than one tenth of claws in length. First tarsal chaetotaxy; ± 12; ± 12; 3–5. Chaetotaxy of hind tarsus I usually 4 or 5 in apterae and 3 or 4 in alatae.

Siphunculi present or absent, when present placed on more or less hairy cones. Cauda broadly rounded. Abdominal tubercles absent. True apterae and slightly alatiform apterae without any dorsal abdominal pigmentation except on seventh and eighth tergites, on which there are often pigmented bars. Alatae and some alatiform apterae with both dorsal and lateral pigmented areas on each abdominal segment. Each segment bearing a dorsal transverse pigmented bar, sometimes broken in the mid-dorsal line, particularly on anterior segments, and a pair of roughly circular lateral sclerites. Lateral sclerites of fifth and sixth abdominal segments of *Neotrama* and *Protrama* fused to bear the siphunculi.

Most of the characters that have usually been used to separate species vary with the degree of alatiformity. The more important characters varying thus are, the suture of the frons, the ratio processus terminalis/base of sixth antennal segment, the ratio hind tarsus/hind tibia and the degree of pigmentation. This fact has greatly contributed to the taxonomic confusion in the group. The characters used are shown in fig. 1.

Systematic Position.

The Tramini appear to be most closely related to the Lachnini. *Protrama* appears to be the most primitive genus of the Tramini morphologically, because the arrangement of the rhinaria and the form of the siphunculi more closely resemble those of the Lachnini than do those of *Neotrama* and *Trama* and by behaviour, as *Protrama* is much more independent of ants than is either *Neotrama* or *Trama*. *Neotrama* has usually been considered synonymous with, or closely related to *Protrama*, the reason being that both these genera have siphunculi, which are absent in *Trama*. The presence of siphunculi is about the only character that *Neotrama* and *Protrama* have in common, apart from the characters of the Tramini as a whole; moreover the structure of the siphunculi differs in *Protrama* and *Neotrama*. The absence of siphunculi in *Trama* is thought to represent a loss, and as *Trama* and *Neotrama* are otherwise almost identical, a close relationship between *Neotrama* and *Protrama* would imply a lineage *Protrama-Neotrama-Trama*. As the siphunculi of *Neotrama* differ from those of *Protrama* and are in some ways better developed, the presence or absence of siphunculi in the Tramini is considered to be an indication of a stage in development rather than an indication of relationship. It is considered that *Trama* and *Neotrama* are closely related, differing almost

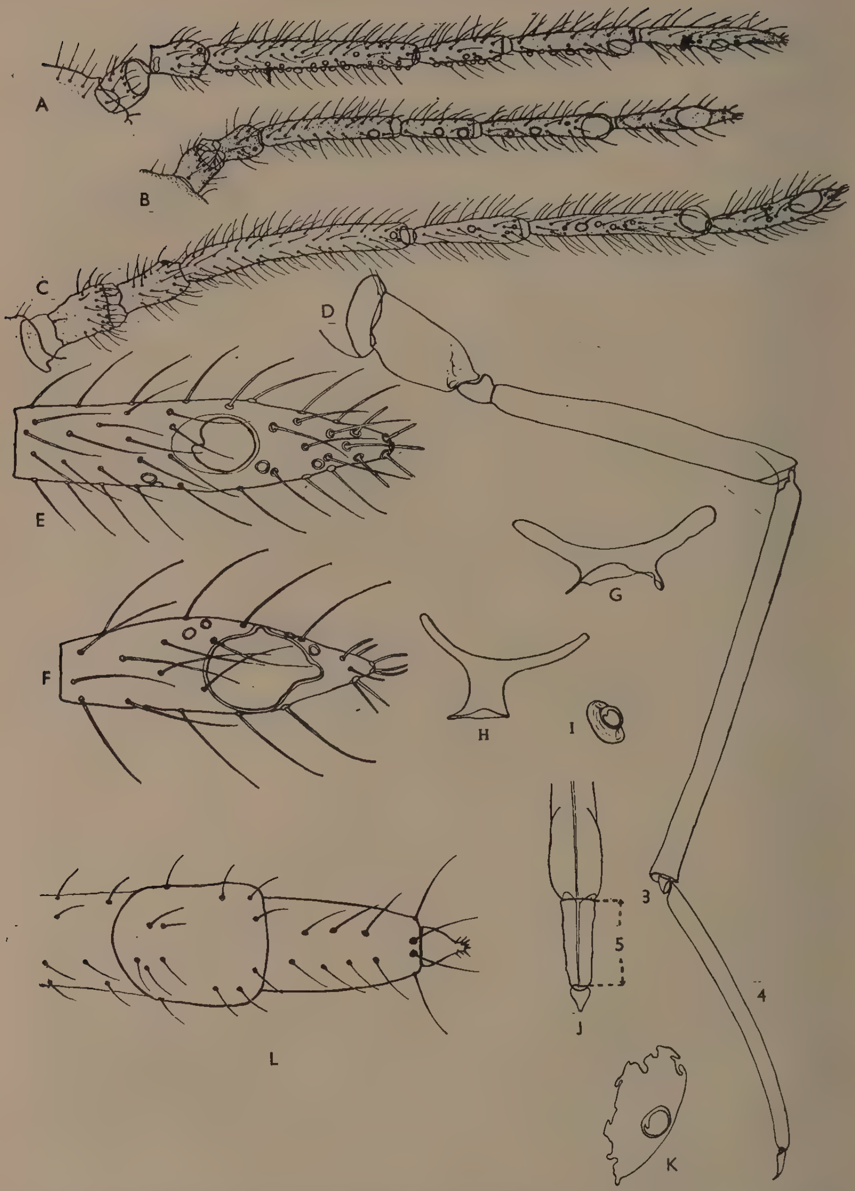

FIG. 1.—A. *Protrama ranunculi* Guercio, antenna of alata. B. *Neotrama caudata caudata* Guercio, antenna of alata. C. *Trama troglodytes* Heyden, antenna of alata. D. Hind leg of Tramini: 3, first tarsal segment, 4, second tarsal segment. E. *Protrama*, sixth antennal segment. F. *Neotrama caudata* s. sp. *maritima*, sixth antennal segment. G and H. Mid-thoracic furcae: G, almost sessile, H, with slender base. I. Siphunculus of *Neotrama*. J. Apex of rostrum showing, (5), ultimate rostral segment. K. Siphunculus of alatiform aptera of *Protrama*. L. *Protrama flavescens* Koch, apex of rostrum showing the seven dorsal rostral hairs.

only in the presence or absence of siphunculi, and constitute a natural group, the sub-tribe Tramina, that has lost many of the Lachnid characters retained in the sub-tribe Protramina.

The tribe Tramini contains three known genera, two of which show considerable specificity in their choice of food plants. *Protrama* is confined to the Cynareae, to the Artemisia-group of the Anthemideae and to *Ranunculus* spp. *Neotrama* is confined to the Ligulatiflorae in the author's experience, but species have been described from *Phaseolus* and perhaps *Rumex*. *Trama* occurs on the roots of most of the major groups of Compositae, but probably not on those of any other family.

Distribution.

Tramini are recorded from Europe, Asia (Siberia to Japan), North Africa and one species from North America. There are no known records from the Southern Hemisphere.

KEY TO THE SUB-TRIBES OF THE TRIBE TRAMINI.

Alatae with 25 to 50 rhinaria on third antennal segment and with sixth antennal segment as long as fifth or longer. Apterae always with siphunculi which are placed on only slightly elevated cones. Processus terminalis at least a quarter (usually more) of the base of the sixth antennal segment in length and bearing six or more normal antennal hairs in addition to the short terminal setae. Dorsal abdominal pigmentation only very rarely absent. On *Ranunculus*, Cynareae, and Anthemideae . . . . **Protramina**

Alatae with 0 to 5 rhinaria on third antennal segment. Apterae and alatae with fifth antennal segment longer than sixth. Siphunculi absent or present; when present they are placed on distinctly elevated cones. Live only on Ligulatiflorae (British species at least). Processus terminalis one quarter or less of the base of the sixth antennal segment in length and without any, or rarely with one, normal antennal hairs in addition to the short terminal setae. On many Compositae . . . . **Tramina**

THE SUB-TRIBE PROTRAMINA.

The characters of this sub-tribe are those of its only known genus, *Protrama* Baker, 1920.

Protrama Baker, 1920.

1843, Kaltenbach, J. H., *Trama*, partim; 1856, Koch, C. L., *Trama*, partim; 1860, Passerini, G., *Trama*; 1872*a*, Ferrari, P. M., *Lachnus*, partim; 1881, Buckton, G. B., *Trama*, partim; 1899, Guercio, G. Del, *Trama*; 1909, Guercio, G. Del, *Trama*, partim; 1920, Baker, A. C., *Protrama*; 1929, Theobald, F. V., *Protrama*; 1929, Nevsky, V. P., *Protrama*, ? partim; 1932, Börner, C., *Protrama*, partim; 1934, Hille Ris Lambers, D., *Protrama*, partim; 1935, Mordwilko, A., *Trama*, partim; 1948, Mordwilko, A., *Trama*, partim; 1952, Börner, C., *Protrama*, partim.

Morphology.

Head of alatae and of most apterae distinctly divided; in some apterae the suture faint and absent in true non-alatiform apterae. Eyes of both apterae and alatae large and of many facets and triommatidion placed posteriorly so as to be easily visible from above. Alatae with numerous rhinaria arranged along one side of antennal segments III to VI. True apterae without secondary rhinaria but, as most specimens are slightly alatiform, some secondary rhinaria usually present, particularly on distal segments and on distal part of III. Processus terminalis at least half as long as base of VI in alatae and from about one-third to three-quarters of it in alatiform apterae. Processus terminalis bearing six or more normal antennal hairs in addition to short terminal setae. Entire length of sixth antennal segment usually much longer than fifth, but in rare true apterae it may be slightly shorter. Ultimate rostral segment with six to twelve dorsal rostral hairs in addition to the three apical pairs and the more numerous lateral and ventral hairs.

Media of fore wing once or twice branched in true alatae, but sometimes simple in brachypterae. Mid-thoracic furca almost sessile. Hind tarsi from one-half to nine-tenths of hind tibiae in length.

Siphunculi always present and placed on slightly elevated cones, which usually appear large as they are fused to pigmented lateral sclerites of fifth and sixth abdominal segments of alatae and alatiform apterae. In true apterae siphunuli appear as mere rings on a very small pigmented base. Segmentally arranged dorsal pigmented bars and lateral sclerites present in alatae and alatiform apterae on all abdominal segments. Dorsal bars distinct from lateral sclerites on segments 1 to 6 but fused with them on 7 and 8. Abdomen of true apterae unpigmented except for the small areas at base of siphunculi already described, sub-genital and anal plates, cauda and sometimes a small transverse bar on the eighth tergite.

Biology.

Protrama is confined to the Cynareae, Anthemideae, and to *Rauunculus* spp. *Protrama flavescens* and *P. ranunculi* produce alatae much more readily than do *P. radicis* and *Trama* spp. This is apparent both in cultures kept in the laboratory, colonies found in the field and in trap catches in districts where *Trama* is known to be plentiful on roots. The true apterae of *P. flavescens* and *P. ranunculi* are unknown, as are the alatae of *P. radicis*.

Notes.

Some records of *Protrama* spp. apply to *Neotrama*, which have been regarded as larvae of *Protrama*, a form which they very much resemble. The four recognised species of *Protrama* are very similar, and to save needless repetition, the only characters given in the individual descriptions are those that have been used to separate one species from another. Other characters are as given in the generic description.

Geographical Distribution.

Protrama is known only from Eurasia and North Africa. Species have been recorded from Britain, Holland, Italy, Germany, Finland, Sweden, Russia and Tunisia.

Type of the Genus.

The type species of *Protrama* is *Trama radicis* Kaltenbach, 1843, fixed by Baker (1920) at the time of the original description of the genus. Kaltenbach's material consisted of two species, *Protrama radicis* as here understood and *Neotrama caudata*. The original description applies largely to a *Protrama*, the presence of a *Neotrama* being indicated only by the food-plants given and possibly by the relative lengths of the fifth and sixth antennal segments. The only host plant listed by Kaltenbach on which a *Protrama* is known to feed is *Cirsium*, so the name *radicis* must be given to a *Cirsium*-feeding species.

It is not known whether Baker had seen material of this genus when he erected it or whether the description was taken from those of earlier authors.

Key to the British species of Protrama.

Apterae.

1. Hind tarsus/tibia ratio = 0·5–0·7. Hind tibia/IV antennal segment ratio = 6·7–8·2. Dorsal rostral hairs 6 to 10; usually 6 to 9. On Anthemideae and *Ranunculus* spp. . . . . 2.
Hind tarsus/tibia ratio = 0·72–0·90. Hind tibia/IV a.s. ratio = 5·1–6·4. Dorsal rostral hairs 8–12. On Cynareae. . . . **P. radicis** (Kaltenbach)
2. Hind tibia/III antennal segment ratio = 2·7 to 3·3. Hind tarsus/tibia ratio = 0·50–0·63. Dorsal rostral hairs 6–10, usually 9. On *Ranunculus* spp. . . . . **P. ranunculi** (Guercio)
Hind tibia/III a.s. ratio = 2·2–2·6. Hind tarsus/tibia ratio = 0·60–0·70. Dorsal rostral hairs 6–8, usually 7. On Anthemideae **P. flavescens** (Koch)

Protrama flavescens (Koch, 1856).

1856, Koch, C. L., *Trama flavescens* ; 1881, Buckton, G. B., ? *Trama troglodytes*, partim ; 1909, Guercio, G. Del, *Trama troglodytes*, partim ; 1913, Theobald, F. V., *Trama donisthorpei* ; 1929, Theobald, F. V., *Protrama donisthorpei* ; 1932, Börner, C., *Protrama radicis*, partim ; 1934, Hille Ris Lambers, D., *Protrama radicum*, partim ; 1935, Mordwilko, A., *Trama radicis*, partim ; 1948, Mordwilko, A., *Trama radicis*, partim ; 1952, Börner, C., *Protrama ranunculi*, partim.

Morphology.

True apterae. Unknown.

Alatiform apterae. Hind tarsus/hind tibia ratio = 0·60–0·67. Hind tibia/IV antennal segment ratio = 6·7–8·2. Mid femur/III a.s. ratio = 1·1–1·3. III a.s./ultimate rostral segment ratio = 2·35–2·90. Dorsal rostral hairs few, 6–8 in number.

Brachypterae. Intermediates between apterae and alatae are common in *P. flavescens*. The rhinarial numbers and ratios between antennal segments of these intermediates vary between the values for alatiform apterae and true alatae.

Measurements of alatiform apterae.

	Body length.	Hind tarsus II.	Hind tibia.	Mid femur.	Ultimate rostral segment.
1.	2·78	0·85	1·30	0·62	0·20
2.	2·88	0·92	1·38	0·67	0·20
3.	3·07	0·98	1·46	0·71	0·22
4.	3·04	0·87	1·29	0·65	0·21

	Length of antennal segments.				Secondary rhinaria on—	
	III.	IV.	V.	VI.	III a.s.	IV a.s.
1.	0·52	0·20	0·27	0·19+0·09	6–8	3–4
2.	0·53	0·22	0·30	0·21+0·12	2–1	3–5
3.	0·61	0·21	0·30	0·25+0·10	24–17	5–3
4.	0·54	0·21	0·30	0·22+0·12	10–8	4–5
5.	0·56	0·21	0·30	0·22+0·12	4–2	4·3

(All lengths in mm.)

Data for measured specimens: 1–3, *Artemisia vulgaris*, Cambridge, 1, 9/iv/51; 2 and 3, 13/xii/50; 4 and 5, *Artemisia* sp., Cambridge (Botanical Gardens), 15/xii/50.

Alatae.—Secondary rhinaria present on antennal segments III, IV, V and VI, in number, III, 25–50; IV, 3–8; V, 3–5; VI, 1–4 in addition to the accessory rhinaria. Media of the fore wing once branched. Hind tarsus/hind tibia ratio = 0·62–0·67; hind tibia/IV antennal segment ratio = 6·3–7·6; hind tibia/III a.s. ratio = 2·2–2·5; III a.s./IV a.s. ratio = 2·7–3·2; III a.s./V a.s. ratio = 1·8–2·2; III a.s./VI a.s. ratio = 1·6–1·9.

Measurements of alatae.

	Body length.	Hind tarsus II.	Hind tibia.	Length of antennal segments.			
				III.	IV.	V.	VI.
1.	3·49	1·05	1·44	0·63	0·22	0·33	0·25+0·10
2.	2·94	0·88	1·36	0·58	0·19	0·28	0·21+0·10
3.	2·92	0·91	1·34	0·60	0·23	0·31	0·21+0·10
4.	3·35	0·88	1·37	0·61	0·20	0·31	0·21+0·11
5.	3·00	0·86	1·38	0·58	0·19	0·30	0·22+0·09

Secondary rhinaria on antennal segment:

	III.	IV.	V.	VI.
1.	48–42	7–5	5—	4–4
2.	36–35	7–6	5–5	2–2
3.	41–35	6–6	5–3	2–4
4.	46–36	6–5	6–5	1–2
5.	34–39	4–3	4–6	3–2

(All lengths in mm.)

Data for measured specimens: 1, *Artemisia annua*, Cambridge, 8/xii/50; 2–4, *Artemisia vulgaris*, Cambridge, 2, 27/xi/50; 3, 30/v/51; 4, 16/x/51; 5, *Artemisia vulgaris*, Wageningen, Holland, 4/vii/46 (*leg. H. R. L.*).

Biology and Transference Experiments.

P. flavescens from *Artemisia annua* has been transferred to *Artemisia vulgaris*. Material from *Artemisia vulgaris* could not be transferred to *Centaurea nigra*, *C. scabiosa*, *Cirsium arvense*, cultivated chrysanthemums or to *Ranunculus repens*. Although *P. flavescens* is very common near Cambridge, it has never been found on cultivated chrysanthemums. There is material in the British Museum of *P. flavescens* said to have been found on *Chrysanthemum*. It is thought that this material either represents a distinct race of aphid, or that only certain varieties of *Chrysanthemum* are attacked or that the host plant of the museum material was wrongly identified.

Geographical Distribution.

Many of the continental records of *P. radicis* apply to this species and it appears to be one of the commonest British species where *Artemisia* is abundant. *P. flavescens* is recorded (often as *P. radicis*) from Russia, Germany, Italy, and England. In England it is known from the Isle of Wight (Theobald, as *P. donisthorpei*) and has been found near Cambridge on *Artemisia annua* and *A. vulgaris* by the author.

Notes.

P. flavescens (as *P. radicis*) has been separated from *P. ranunculi* by Mordwilko on the ratio of the fifth and sixth antennal segments. Mordwilko states that the sixth antennal segment is distinctly longer than the fifth in *ranunculi* and is only slightly longer in *flavescens*. This character may be used safely for the normal alatiform apterae, but the rarely found only slightly alatiform apterae of *ranunculi* have a shorter sixth antennal segment, giving a ratio with the fifth like that of the alatiform apterae of *flavescens*.

Protrama longitarsus (Ferrari, 1872).

1872*a*, Ferrari, P. M., *Lachnus longitarsus*; 1935, Mordwilko, A., ? *Trama radicis*, partim.

Morphology.

True apterae.—Unknown.

Alatiform apterae.—Described from two specimens. Very like *P. ranunculi* and apparently differing from it only in that hind tibiae and antennae are rather longer than in *ranunculi* and ultimate rostral segment rather shorter. This gives a hind tibia/ultimate rostral segment ratio = about 6·8 (in *P. ranunculi* 5·7–6·5). Body length of *longitarsus* only about two and a third times the sum of the lengths of antennal segments III, IV, V and VI (in *ranunculi*, 2·5–2·8). *P. longitarsus* differs from *flavescens* and *radicis* by the same characters as does *ranunculi*, including the number of dorsal rostral hairs.

Measurements of alatiform apterae.

	Bod length.	Hind tarsus II.	Hind tibia.	Mid femur.	Ultimate rostral segment.	Length of antennal segments.				Rhinaria on antennal segments.	
						III.	IV.	V.	VI.	III.	IV.
1.	3·53	0·94	1·77	0·77	0·26	0·56	0·23	0·33	0·39	5–3	3–4
2.	3·48	0·87	1·65	0·75	0·25	0·56	0·21	0·32	0·34	0–1	4–3

(All lengths in mm.).

Data for measured specimens: *Artemisia campestris*, Airolo, Switzerland, 22/v/50 (*leg. H. R. L.*).

Alatae.—Unknown.

Geographical Distribution.

P. longitarsus is known only from Italy (original description), Switzerland (material from Dr. Hille Ris Lambers) and perhaps from Russia, under the name of *P. radicis* (Mordwilko, 1935). The lack of records from other countries where *Artemisia campestris* is common is probably due to confusion with closely related and very similar species.

Notes.

Ferrari described *Lachnus longitarsus* twice in 1872. In the original description (page 80) a *Protrama* from *Artemisia campestris* is described, but on page 233 there is another description, this time of material from *Phaseolus* *vulgaris*. The latter description applies better to a *Neotrama* than to a *Protrama*. *Lachnus longitarsus* Ferrari, 1872, when refound, will require a new name if it is distinct from *Tactilotrama antennata* (Mordw.).

Only two specimens of *P. longitarsus* have been seen by the author, both alatiform apterae collected by Dr. Hille Ris Lambers in Switzerland. As these are the only two adult specimens of *Protrama* seen from Switzerland and also the only ones seen from *Artemisia campestris*, no attempt has been made to include *longitarsus* in the key to species.

Protrama radicis (Kaltenbach, 1843).

1843, Kaltenbach, J. H., *Trama radicis*, partim ; 1881, Buckton, G. B., ? *Trama troglodytes*, partim ; 1907, Guercio, G. Del, *Trama troglodytes*, partim ; 1920, Baker, A. C., ? *Protrama radicis* ; 1929, Theobald, F. V., *Protrama radicis*, partim ; 1932, Börner, C., *Protrama radicis*, partim ; 1934, Hille Ris Lambers, D., *Protrama radicum*, partim ; 1952, Börner, C., *Protrama radicis*.

Morphology.

True apterae.—Head not divided and antennae without secondary rhinaria. No dorsal abdominal pigmentation except at base of siphunculi. Siphuncular cones very small, being less than three times siphuncular porus in diameter. Hind tarsus/hind tibia ratio varies from 0·86 to 0·89. Fifth antennal segment as long as or even very slightly longer than sixth (measured aptera no. 1).

This form looks very like a *Neotrama*, but may be separated by the form of the siphuncular cones and by the hairs on the processus terminalis. Found only once on *Cynara scolymus* in April and May, together with some slightly alatiform specimens. Only very slightly alatiform apterae of *P. radicis* have been found on *Cirsium arvense* at the end of December and in January.

Alatiform apterae.—Head divided and antennae usually with secondary rhinaria. Each abdominal segment bears pigmented dorsal and lateral sclerites, lateral sclerites of fifth and sixth abdominal segments being fused with siphuncular cones. Hind tarsus/hind tibia ratio = 0·72–0·87 ; hind tibia/III a.s. ratio = 2·2–2·9 ; hind tibia/IV a.s. ratio = 5·2–6·4 ; mid femur/III a.s. ratio = 1·25–1·55 ; III a.s./ultimate rostral segment = 1·65–2·15. Dorsal rostral hairs usually 10, 11 or 12.

Measurements of apterae.

	Body length.	Hind tarsus II.	Hind tibia.	Mid femur.	Ultimate rostral segment.	Length of antennal segments.				Secondary rhinaria on antennal segments.	
						III.	IV.	V.	VI.	III.	IV.
1.	3·05	1·00	1·15	0·63	0·27	0·48	0·18	0·25	0·18+0·07	0–0	1–0
2.	2·88	1·03	1·25	0·65	0·26	0·49	0·25	0·27	0·20+0·11	0–0	0–1
3.	3·38	1·01	1·25	0·68	0·28	0·53	0·23	0·29	0·31	1–1	2–2
4.	3·07	0·97	1·26	0·67	0·26	0·51	0·23	0·28	0·29	0–0	2–2
5.	3·11	0·86	1·02	0·59	0·25	0·42	0·19	0·26	0·30	1–1	3–3

Data for measured specimens : 1, *Cynara scolymus*, Cambridge, 30/iv/51 (non-alatiform) ; 2–4, *Cirsium arvensis*, 2 and 3, Cambridge 20–22/x/50 ; 4, Barton Mills, Suffolk, 8/ix/49 (*leg. H. L. G. S.*) ; 5, *Arctium lappa*, East Chinnock, Somerset, 3/ix/50.

Alatae.—Unknown.

Host Plants.

Arctium lappa, *Carduus marianus*, *Centaurea scabiosa*, *Cirsium arvensis*, *Cynara scolymus*. The many records of Ligulatiflorae as hosts of this species are thought to be in error, the species concerned being a *Neotrama*.

Biology.

It is probable that *P. radicis* as here conceived is a complex of sub-species, kleinarten or races, as material from one host plant could not be transferred to another. Material from *Cynara* refused *Cirsium arvensis* and *Centaurea scabiosa*. Material from *Cirsium arvensis* could not be transferred to *Arctium lappa* or to *Centaurea scabiosa*. The single large collection from *Arctium lappa* has on the average fewer dorsal rostral hairs than is usually found in material from *Cynara* and *Cirsium*.

Notes.

Kaltenbach suggested that his *radicis* was a synonym of *radicum* Fonscolombe, 1841. This opinion was accepted by Hille Ris Lambers when he sank *radicis* Kalt. 1843 under *radicum* Fonsc. 1841. Fonscolombe's description is thought to apply more closely to a *Tetraneura* or closely related genus, an opinion held by Lichtenstein (1885) and Mordwilko (1921). Theobald (1929) says " It might be a *Forda*," but this is not thought to be correct as Fonscolombe mentions the presence of siphunculi which are absent in *Forda*. Material labelled *Trama radicis* in Buckton's collection (material obtained from Walker) is the species here regarded as *Neotrama caudata*. In his monograph of British Aphids Buckton places *radicis* as a synonym of *Trama troglodytes*. It is not known whether Baker (1920) described the genus *Protrama* from material or from the descriptions of earlier authors. If he had material it is not known which species he possessed.

Geographical Distribution.

Many of the records of *radicis* apply to *flavescens*. *P. radicis* certainly occurs in Germany, Italy and England, but it seems to be rarer than both *P. flavescens* and *ranunculi*. The rarity of *P. radicis* is not the only reason for the lack of knowledge of alatae, as the few known colonies in Cambridge have been kept under observation and apparently never produced either very alatiform apterae or true alatae. Alatae of this species have never been seen in trapped material. The lack of alatae may be one of the reasons for its rarity. In Britain *radicis* is recorded from Kent (Theobald), and material has also been seen from Cambridge and Suffolk on *Cirsium* (*leg. H. L. G. S.*), from Pembroke on *Centaurea scabiosa* (*leg. Dr. I. Thomas*), and it has been found in Somerset on *Arctium*, *Carduus* and *Cirsium*.

Protrama ranunculi (Guercio, 1909).

1906, Schouteden, N., *Trama radicis* ; 1909, Guercio, G. Del, *Trama ranunculi* (? partim, the alatae) ; 1929, Theobald, F. V., *Protrama radicis*, partim ; 1932, Börner, C., *Protrama radicis*, partim ; 1934, Hille Ris Lambers, D., *Protrama radicum*, partim ; 1935, Mordwilko, A., *Trama ranunculi* ; 1948, Mordwilko, A., *Trama ranunculi* ; 1951, Heikinheimo, O., *Protrama ranunculi* ; 1952, Börner, C., *Protrama ranunculi*, partim.

Morphology.

True apterae.—Unknown.

Alatiform apterae.—Head divided and antennae usually with secondary rhinaria. Abdomen with dorsal and lateral pigmented sclerites. Hind tarsus/hind tibia ratio = 0·50–0·63; hind tibia/IV antennal segment ratio = 6·9–8·1; mid femur/III a.s. ratio = 1·3–1·7; III a.s./ultimate rostral segment ratio = 1·7–2·2. Dorsal rostral hairs 6 to 10, usually 9. Body length usually two and a half times or more the sum of the lengths of antennal segments III, IV, V and VI.

Measurements of alatiform apterae.

	Body length.	Hind tarsus II.	Hind tibia.	Mid femur.	Ultimate rostral segment.
1.	3·70	0·82	1·63	0·78	0·26
2.	3·13	0·83	1·47	0·69	0·25
3.	3·58	0·88	1·59	0·73	0·24
4.	3·26	0·85	1·52	0·70	0·23
5.	3·27	0·85	1·51	0·69	0·25

	Length of antennal segments.				Rhinaria on antennal segments.	
	III.	IV.	V.	VI.	III.	IV.
1.	0·55	0·25	0·30	0·30	4–6	6–5
2.	0·47	0·21	0·25	0·32	6–4	5–4
3.	0·52	0·22	0·29	0·31	15–10	4–6
4.	0·52	0·21	0·29	0·35	9–14	5–5
5.	0·51	0·22	0·26	0·21+0·13	3–0	3–2

Data for measured specimens; all on *Ranunculus* spp., 1–3, Reading, Berks., 1 and 2, 29/v/50; 3, 18/vi/49; 4, Bennekom, Holland, 3/vii/49 (*leg. H. R. L.*); 5, St. Pietersburg, Holland, 5/ix/39 (*leg. H. R. L.*).

Alatae.—Media of forewing twice branched. Hind tarsus/hind tibia ratio = 0·50–0·57; hind tibia/III antennal segment ratio = 2·9–3·3; hind tibia/ IVa.s. ratio = 7·3–8·8; mid femur/III a.s. ratio = 1·4–1·8; III a.s./IV a.s. ratio = 2·3–2·8; III a.s./V a.s. ratio = 1·6–2·1; III a.s./VI a.s. ratio = 1·40–1·75. Secondary rhinaria, III, 28–45; IV, 4–8; V, 2–7; VI, 2–4 + accessory rhinaria.

Measurements of alatae.

	Body length.	Hind tarsus.	Hind tibia.	Length of antennal segments.				Rhinaria on antennal segments.			
				III.	IV.	V.	VI.	III.	IV.	V.	VI.
1.	2·78	0·82	1·49	0·47	0·20	0·29	0·22+0·11	31–30	6–6	5–6	3–3
2.	2·51	0·80	1·44	0·46	0·19	0·27	0·19+0·12	33–35	7–8	5–5	2–2
3.	3·25	0·82	1·49	0·48	0·20	0·29	0·20+0·12	32–30	7–8	4–7	3–3
4.	2·92	0·82	1·56	0·50	0·21	0·28	0·18+0·13	39–44	8–7	6–6	1–2
5.	3·15	0·86	1·68	0·52	0·22	0·26	0·21+0·12	36–31	4–5	2–3	1–2

Data for measured specimens: all on *Ranunculus* spp., 1–3, Reading, Berks., 1 and 2, 29/v/50; 3, 3/vi/50; 4, Wageningen, Holland, 22/ix/34 (*leg. H. R. L.*); 5, St. Pietersburg, Holland, 5/ix/39 (*leg. H. R. L.*).

Host Plants.

Ranunculus repens and rarely *R. bulbosus.*

Biology.

Numerous attempts to tranfer *P. flavescens* to *Ranunculus repens* at different seasons of the year and a smaller number of attempts to transfer *P. ranunculi* to *Artemisia vulgaris* in early summer invariably gave negative results. *P. flavescens* would not settle down on *Ranunculus*. *P. ranunculi* would sometimes feed on *Artemisia*, but young produced never reached maturity.

Geographical Distribution.

P. ranunculi is recorded from Italy (Guercio), Holland (material from H. R. L.), Finland (Heikinheimo) and Britain. British material has been seen from Pottern, Wilts. (British Museum) and found in Cambridge and Berkshire. The specimens trapped at Rothamsted and recorded as *P. radicum* (Johnson and Eastop, 1951) are *P. ranunculi.*

THE SUB-TRIBE TRAMINA.

Morphology.

Head usually divided, although not always distinctly so, the suture being absent in true apterae. Eyes large and of many facets in alatae, with triommatidion placed postero-ventrally so as to be little visible from above. Eyes of apterae variable, as in alatae, smaller compound eyes or only a triommatidion. Alatae with only 0 to 5 rhinaria on third antennal segment. Processus terminalis short, a quarter or less of the base of sixth antennal segment in length and without or with only one normal antennal hair in addition to the short terminal setae. Media of fore wing usually once branched, but sometimes simple or twice branched. Hind tarsi from three fifths to equal the hind tibiae in length. Fifth antennal segment always longer than sixth and usually distinctly so.

Siphunculi absent (*Trama*) or present (*Neotrama*). When present siphunculi are small elevated, and in apterae rarely pigmented, cones with concave margins. Siphuncular cones bear only a few hairs and these confined to the base. Alatae with both dorsal and lateral pigmented areas, as in *Protrama*. Apterae only exceptionally with any dorsal abdominal pigmentation on other than seventh and eighth tergites, each of which often bears a pigmented band.

Notes.

The Tramina has two known genera that appear to differ only in the presence or absence of siphunculi, and in that the alatae of *Neotrama* usually have more rhinaria on the third antennal segment (3 or 4) than do those of *Trama* (0 to 2). The alatae of *Trama* do not have siphunculi, as was stated by Theobald (1929), his single specimen being a *Neotrama.*

Geographical Distribution.

Trama is recorded from North America, Europe, Siberia and Japan. *Neotrama* is known only from Europe and possibly (as *Trama antennata* and some records of *Trama radicis*) from Turkestan and western Asia.

Key to the genera of the sub-tribe Tramina.

Siphunculi present	**Neotrama** Baker
Siphunculi absent	**Trama** Heyden

Trama antennata may come in the genus *Neotrama* or may be distinct. (It is the type species of *Tactilotrama* Börner, 1952, placed as a sub-genus of *Protrama*, as was *Neotrama* Baker.) The character given by Mordwilko (1931) for the identification of *antennata*, hairs of two different lengths on the legs, separates it from all known *Tramini*.

Neotrama Baker, 1920.

1843, Kaltenbach, J. H., *Trama*, partim ; 1852, Walker, F., *Trama*, ? partim ; 1872*b*, Ferrari, P. M., *Lachnus* ; 1881, Buckton, G. B., *Trama*, partim ; 1909, Guercio, G. Del, *Trama*, partim ; 1920, Baker, A. C., *Neotrama* ; 1929, Theobald, F. V., *Neotrama* and *Trama*, partim (the alatae) ; 1932, Börner, C., *Protrama*, partim ; 1934, Hille Ris Lambers, D., *Protrama*, partim ; 1935, Mordwilko, A., *Trama*, partim ; 1944, Börner, C., *Protrama*, partim ; 1948, Mordwilko, A., *Trama*, partim ; 1952, Börner, C., *Neotrama* (as a sub-genus of *Protrama*), partim, and *Protrama* s. str., partim.

Morphology.

Differs from *Trama* only in presence of siphunculi, in that apterae usually have eyes of many facets (12 +), and in that alatae of *Neotrama* usually have three or four rhinaria on third antennal segment. Other characters as for sub-tribe Tramina.

Trama antennata is tentatively placed in this genus, in the sub-genus *Tactilotrama* Börner, 1952. When material of this species is available for study it may be found deserving of full generic rank. It is discussed in the section on species not seen by the author.

Biology.

The only hosts from which this genus has been seen come in the Cichoreae (or Ligulatiflorae) of the family Compositae. There are records of species from *Rumex* and *Phaseolus*, but neither of these have been seen by the author.

Alatae are produced at all times of the year but are most frequent in the autumn.

Geographical Distribution.

Neotrama is known for certain only from Western and Central Europe, but probably occurs also in Eastern Europe and Western Asia. *Longitarsus taraxaci* Shinji, 1921, from Japan may come in this genus, but the original description has not been seen.

Type of the Genus.

Trama caudata Guercio, 1909 (as *Neotrama delguercioi* Baker, 1920, nom. nov. pro *Trama troglodytes* Guercio, 1909 nec Heyden, 1837). The original description of *N. delguercioi* (as *Trama troglodytes* Guercio nec Heyden) is of a mixture of three species, *Neotrama caudata* as here understood, *Protrama flavescens* and *P. radicis*. This is the same mixture of genera as that from which Kaltenbach described *Protrama radicis*, the type of *Protrama*. As most of Del Guercio's description applies to a *Neotrama* and only a figure of a siphunculus is definitely ascribable to *Protrama*, the name *Neotrama* may be applied in the present sense, which, from his generic description, is obviously the way Baker intended. It is thought most probable that Baker had never seen material of this genus when he erected the name.

With the exception of Theobald (1929) and Börner (1952), *Neotrama* has not been recognised, presumably because of the confusion about the type species and the resemblance of adult *Neotrama* to larval *Protrama*. Börner (1952) regards *Neotrama* as a sub-genus of *Protrama* and applies the name *flavescens* Koch to *Neotrama formicella* Theob., and regards the *Artemisia* feeding *Protrama* as a synonym of *P. ranunculi*, quoting transference experiments of F. P. Müller. *Trama caudata* Guercio, here regarded as the correct name for the type species of *Neotrama*, is placed by Börner in *Protrama*, s. str.

Key to the sub-genera of the genus Neotrama.

Legs bearing hairs of two different lengths . . . . . **Tactilotrama** Börner
Legs with all hairs of the same length . . . . **Neotrama** s. str.

For notes on *Tactilotrama* see the section on species not seen by the author.

Neotrama Baker, s. str.

Only one species is recognised, *N. caudata* (Guercio), which is regarded as having two sub-species, *N. caudata* s. str. and *N. caudata maritima* subsp. n. For the characters of *N. caudata* s. lat. see the generic description of *Neotrama* and the separate descriptions of the two sub-species.

Key to the sub-species of Neotrama caudata *s. lat.*

III antennal segment/IV a.s. ratio = 0·9–1·35 (usually 1·0–1·25); III a.s./IV a.s. ratio = 1·8–2·35 (usually 2·0–2·2). Found inland, often in cultivated ground . . . . **N. caudata** s. str.
III a.s./V a.s. ratio = 1·4–1·8 (usually 1·5–1·7); III a.s./IV a.s. ratio = 2·2–2·8 (usually 2·4–2·7). On plants growing behind sand dunes and on cliffs by the sea . . . . **N. caudata maritima** subsp. n.

The alatae of the sub-species *maritima* are not known but, as the apterae and alatae of *caudata* s. str. have similar antennal segment ratios, it is thought that the above key will separate alatae as well as apterae.

Neotrama caudata (Guercio, 1909) sensu stricto.

1843, Kaltenbach, J. H., *Trama radicis*, partim; 1852, Walker, F., *Trama troglodytes*; 1881, Buckton, G. B., *Trama troglodytes*, ? partim; 1909, Guercio, G. Del, *Trama troglodytes*, partim, *T. caudata* and *T. horvathi*; 1920, Baker, A. C., *Neotrama delguercioi*; 1929, Theobald, F. V., *Trama troglodytes*, partim (alata) and *Neotrama formicella*; 1932, Börner, C., *Protrama radicis*, partim; 1934, Hille Ris Lambers, D., *Protrama radicum*, partim; 1935, Mordwilko, A., *Trama radicis*, partim, *T. delguercioi*, *T. horvathi*, *T. caudata*; 1948, Mordwilko, A., *Trama radicis*, partim; 1952, Börner, C., *Protrama caudata*, *Neotrama flavescens*.

Morphology.

Apterae.—Body colour pale yellow or white in life. Antennal segment ratios as given in key to sub-species. Hind tarsus/hind tibia ratio about 0·75–0·85. Very alatiform apterae and brachypterae rare in this species, but when they do occur the first alatiform characters to appear are the antennal and thoracic structures. Abdominal pigmentation of alatae never occurs in individuals without any wings, as it does in *Protrama.*

Measurements of apterae.

						Length of antennal segments.				Secondary rhinaria on—			
	Body length.	Hind tarsus.	Hind tibia.	Mid femur.	Ultimate rostral segments.	III.	IV.	V.	VI.	III.	IV.	V.	VI.
1.	2·61	0·72	0·88	0·51	0·20	0·30	0·14	0·28	0·26	0	0–1	2–1	0
2.	2·53	0·70	0·83	0·49	0·21	0·31	0·16	0·28	0·26	0	1–1	3–1	0
3.	2·66	0·72	0·85	0·48	0·20	0·33	0·15	0·32	0·27	0	1–1	2–1	0
4.	2·98	0·78	0·96	0·55	0·25	0·38	0·20	0·29	0·25	0	1–2	3–3	0
5.	3·31	0·73	0·87	0·53	0·21	0·30	0·15	0·28	0·25	0	1–1	1–3	0

Data for measured specimens : 1 and 2, *Sonchus asper*, 1, Harpenden, Herts., 1/x/50 ; 2, Cambridge, 5/xii/50 ; 3, *Taraxacum officinale*, Cambridge, 12/x/50 ; 4, *Hypochoeris radicata*, West Byfleet, Surrey, 16/v/51 (*leg. H. L. G. S.*) ; 5, *Cichorium endiva*, Amerongen, Holland, 15/x/50 (*leg. H. R. L.*).

Alatae.—Distribution of secondary rhinaria on antennae : III, 1–5 (usually 3 or 4) ; IV, 2–3 ; V, 2–5 ; VI, 0–2 + accessories. In ratios of lengths of antennal segments apterae and alatae very similar. Media of fore wing usually once branched, but sometimes twice branched or simple. It would seem probable that true alatae have media twice branched, but that most of the alatae produced are slightly brachypterous, just as most of the apterae are to some extent alatiform. Concave margins of siphuncular cones very well shown in alatae, being more heavily pigmented than in apterae.

Measurements of alatae.

				Length of antennal segments.				Secondary rhinaria on—			
	Body length.	Hind tarsus.	Hind tibia.	III.	IV.	V.	VI.	III.	IV.	V.	VI.
1.	2·72	0·81	0·99	0·36	0·18	0·32	0·21+0·06	3–3	2–2	2–2	0–0
2.	2·66	0·80	0·97	0·35	0·19	0·33	0·22+0·05	1–2	3–2	3–3	0–0
3.	2·33	0·68	0·87	0·30	0·17	0·29	0·20+0·04	1–1	2–2	2–2	0–0
4.	2·38	0·73	0·89	0·33	0·18	0·30	0·20+0·05	4–3	2–2	3–3	0–0
5.	3·22	0·78	0·99	0·33	0·18	0·30	0·21+0·04	2–2	2–3	4–3	0–0

Data for measured specimens : 1–4, *Sonchus* sp., Cambridge, 1 and 2, 13/xi/50 ; 3 and 4, 4/xii/50 ; 5, *Cichorium endiva*, Amerongen, Holland, 18/x/50 (*leg. H. R. L.*).

Host Plants.

Material has been seen from *Cichorium endiva*, *Lactuca* sp., *Hypochoeris radicata*, *Picris* (*Helminthia*) *echioides*, *Sonchus asper*, *S. oleraceus*, *Taraxacum officinale*, and is recorded from *Leontodon* sp.

Biology.

Material from *Sonchus asper* has been transferred to *Sonchus oleraceus*, *Taraxacum officinale*, *Hypochoeris radicata* and to cultivated lettuce. Material from *Hypochoeris radicata* was transferred to *Picris echioides*, *Sonchus asper*, *S. oleraceus* and *Taraxacum officinale*. Material found on *Taraxacum officinale* has been transferred to *Sonchus asper*. Material from *Sonchus asper* could not be transferred to *Phaseolus vulgaris* or *Rumex obtusifolia*, either in the summer or the autumn. Neither could material from *Sonchus asper* be transferred to *Artemisia vulgaris* or *Cirsium arvensis*.

Geographical Distribution.

Recorded from Russia (Mordwilko, 1935, as *Trama radicis*), Germany (in original description of *Protrama radicis*), Italy (Del Guercio), France (Peneau, 1926) and England (Theobald, 1929, as *Neotrama formicella*). Material has been seen from Holland (collection of H. R. L.) and from England. In England specimens have been seen from Kent (British Museum); Surrey (*leg. H. L. G. S.*); Herts. (B.M., and *leg. Dr. L. Broadbent*) and has been found in Cambridge.

Notes.

In the original description *caudata* is said to differ from the other Tramini by the shape of the cauda, and the posterior end of the abdomen is figured. Many of Guercio's figures seem to have been drawn from dried material, and a contraction of the apex of the abdomen, together with distortion of the cauda, is a likely result of such treatment. Del Guercio's figures show the body to be covered with very short hairs, which is another character never seen in the Tramini. However, as the short hairs are not mentioned in the description and because of the great variation in the accuracy of many of Del Guercio's other figures, *caudata* is regarded as being the correct name for the common *Neotrama*. In a number of cases Del Guercio's written descriptions and figures do not agree and both differ from his measured specimen. The measurements quoted in the original description of *Trama horvathi* would make this name correct for the material described here as a new sub-species *maritima*. The figure of *horvathi* looks more like a larva of *Protrama radicis* than any other member of the Tramini, except that it is shown as having no siphunculi. Fig. 22 on the same plate is an enlargement of the siphunculus of *horvathi* and obviously belongs to a *Neotrama*. For these reasons *horvathi* is not used for what is here called *maritima*. Unfortunately it is not possible to examine Del Guercio's material as it was destroyed during the war. If it is subsequently found that there is a distinct species with an elongate cauda and short antennal hairs feeding on *Lactuca sativa*, its correct name will be *Neotrama caudata*. It will probably still be the type of *Neotrama* because the figure of *troglodytes* has short antennal hairs, and it was *troglodytes* Guercio nec Heyden, renamed *delguercioi*, which was made the type of *Neotrama* by Baker. In that case *horvathi* Guercio is the correct name for what is called *caudata* in the present work, unless *horvathi* is applied to the maritime species, in which case *Neotrama formicella* Theobald becomes the correct name, assuming that the refound short-haired *caudata* is co-generic with the British species.

The single specimen of *Neotrama formicella*, an aptera, in the Theobald collection, is labelled in Theobald's handwriting "*Neotrama delguercioi* Baker, Islip 13/v/10, nest of *Lasius niger*." It is from a single alata of the same species that Theobald's 1929 description of the alata of *Trama troglodytes* was made. Two slides of Walker's material in Buckton's collection in the British Museum, labelled "*Trama radicis*, Sowthistle, 5/vi/1847" and "30/vi/1847," are also *caudata*. It is also this species recorded as "an apparently undescribed *Protrama* sp." by Broadbent (1951).

N. caudata is common in Hertfordshire and Cambridge on the roots of *Sonchus* spp. growing as weeds of cultivated ground and also occurs on cultivated lettuces.

Neotrama caudata **maritima** subsp. n.

? 1909, Guercio, G. Del, *Trama horvathi*, partim.

Morphology.

Apterae.—A whitish aphid in life and very similar to normal *caudata*, but differing in having longer antennae and different ratios between the segments. Usually larger than *caudata* but difference in antennal ratios is not due merely to an increase in size, as large specimens of *caudata* are as big as *maritima* and may still be separated by the same characters. The antennal ratios giving the greatest separation can be obtained from the key to sub-species and others from the measured apterae.

Measurements of apterae.

	Body length.	Hind tarsus.	Hind tibia.	Mid femur.	Ultimate rostral segment.	Length of antennal segments.				Rhinaria on antennal segments.			
						III.	IV.	V.	VI.	III.	IV.	V.	VI.
1.	2·78	0·97	1·19	0·64	0·25	0·51	0·20	0·32	0·26	0	2–1	2–3	0
2.	3·04	1·01	1·24	0·65	0·25	0·51	0·21	0·32	0·26	0	2–2	4–4	0
3.	3·85	0·98	1·29	0·70	0·25	0·55	0·22	0·35	0·27	0	2–1	2–3	0
4.	3·41	1·01	1·29	0·67	0·26	0·52	0·21	0·34	0·25	0	2–3	2–2	0
5.	2·64	0·75	0·98	0·52	0·22	0·41	0·16	0·26	0·21	0	1–1	1–2	0

Data for measured specimens: 1–4, *Picris* (*Helminthia*) *echioides*, West Bay, Dorset, 6/ix/50; 5, *Sonchus asper*, Herm, Channel Isles, 12/vi/51.

Alatae.—Not known.

Host Plants.

Picris (*Helminthia*) *echioides*, *Sonchus asper* and possibly also *Cichorium endiva*.

Geographical Distribution.

N. caudata maritima is known from the cliffs about a mile to the west of West Bay, Dorset; Herm and Sark in the Channel Isles and possibly also from Vaassen, Holland (*leg. H. R. L.*)

Notes.

The colony from the roots of *Picris echioides* was in the nest of *Lasius umbratus* and consisted of more than thirty adult apterae, one of which was selected as type and is in the collection of the British Museum.

Trama Heyden, 1837.

1837, Heyden, C. H. G. von, *Trama* ; 1857, Koch, C. L., *Trama*, partim ; 1881, Buckton, G. B., ? *Trama*, partim ; 1909, Guercio, G. Del, *Trama*, partim ; 1920, Baker, A. C., *Trama* ; 1929, Theobald, F. V., *Trama*, partim (apterae) ; 1930, Gillette, G. P., and Palmer, M. A., *Trama* ; 1931, Gillette, G. P., and Palmer, M. A., *Trama* ; 1932, Börner, C., *Trama* ; 1935, Mordwilko, A., *Trama*, partim ; 1942, Oestlund, O. W., *Trama* ; 1944, Börner, C., *Trama* ; 1948, Mordwilko, A., *Trama*, partim ; 1952, Börner, C., *Trama*.

Morphology.

Siphunculi absent in both apterae and alatae. Eyes of apterae of three facets or more, very alatiform specimens with large compound eyes as in alatae. Alatae with usually only two or less rhinaria on third antennal segment. Media of fore wing usually once branched but sometimes twice branched or simple. True alatae probably have media twice branched, as in *Neotrama*. Other characters as for the sub-tribe *Tramina*.

Key to the morphologically separable species of Trama.

Apterae.

Hind tarsus/hind tibia ratio = 0·84–0·92, eyes of many facets. On *Taraxacum* (only ?) . . . . **T. rara** Mordwilko
Hind tarsus/hind tibia ratio = 0·65–0·82, eyes of only three facets, if of more then alatiform and hind tarsus/tibia ratio is less than 0·80. On many Compositae including *Taraxacum* . . . . **T. troglodytes** Heyden

Alatae.

Hind tarsus/tibia ratio = 0·77–0·85. On *Taraxacum* . . **T. rara** Mordwilko
Hind tarsus/tibia ratio 0·60–0·73. On many Compositae **T. troglodytes** Heyden

Trama rara Mordwilko, 1908.

1881, Buckton, G. B., ? *Trama troglodytes*, partim ; 1908, Mordwilko, A., *Trama rara* (not seen) ; 1930, Gillette, G. P., and Palmer, M. A., *Trama oculata* ; 1931, Gillette, G. P., and Palmer, M. A., *Trama oculata* ; 1935, Mordwilko, A., *Trama rara*, ? partim ; 1948, Mordwilko, A., *Trama rara*, ? partim ; 1952, Börner, C., *Trama rara*.

Morphology.

Apterae.—Differs from all other species in the genus by the great length of the hind tarsus relative to the hind tibia and by the large size of the eyes of normal apterae. This combination of characters separates *rara* from the alatiform apterae of other species which, although they may have large eyes as in their alatae, will also have the low hind tarsus/hind tibia ratio of alatae. Hind tibia/III antennal segment ratio = 2·45–3·0 ; III a.s./IV a.s. ratio = 1·8–2·5 ; III a.s./V a.s. ratio = 1·2–1·9 ; III a.s./VI a.s. ratio = 1·3–1·8 ; V a.s./VI a.s. ratio = 1·0–1·2. Mesothoracal furca variable, from almost sessile to placed on a long slender base.

Measurements of apterae.

	Body length.	Hind tarsus.	Hind tibia.	Mid femur.	Ultimate rostral segment.	Length of antennal segments.				Rhinaria on antennal segments.			
						III.	IV.	V.	VI.	III.	IV.	V.	VI.
1.	3·44	0·82	1·03	0·64	—	0·44	0·18	0·30	0·26	0	0–0	0–1	0
2.	3·14	0·82	1·03	0·64	0·25	0·41	0·18	0·28	0·25	0	1–2	1–1	0
3.	3·11	0·77	0·93	0·55	0·25	0·40	0·17	0·26	0·22	0	1–1	0–1	0
4.	2·95	0·78	0·92	0·57	0·26	0·39	0·20	0·27	0·26	0	0–1	0–0	0
5.	2·48	0·68	0·87	0·51	0·22	0·36	0·18	0·26	0·25	0	1–0	1–0	0
6.	2·83	0·73	0·85	0·51	0·23	0·35	0·16	0·24	0·23	0	1–1	0–1	0

Data for measured specimens: 1–3, "*Trama oculata*," *Taraxacum officinale*, Fort Collins, Colorado, U.S.A. (*leg. H. R. L.*); 4–6, *Taraxacum* sp., Reading, Berks., 4, 20/iv/48; 5 and 6, 22/iv/49.

Alatae.—Differing from *troglodytes* by the relatively longer hind tarsus. Secondary rhinaria, III, 0–4 (average 1·7); IV, 0–5 (av. 2·4); V, 1–3 (2·2); VI, usually 0 but rarely with one.

Measurements of alatae.

	Body length.	Hind tarsus.	Hind tibia.	Mid femur.	Mid tibia.	Length of antennal segments. III.	IV.	V.	VI.	Rhinaria on antennal segments. III.	IV.	V.	VI.
1.	2·83	0·85	1·08	0·60	0·85	0·44	0·20	0·37	0·25	0–2	4–2	3–2	0–0
2.	2·59	0·87	1·05	0·58	0·81	0·43	0·20	0·30	0·25	1–1	2–3	2—	0—
3.	2·86	0·84	1·04	0·58	0·80	0·44	0·20	0·30	0·26	4–2	3–2	2–3	1–0
4.	2·83	0·86	1·06	0·56	0·84	0·43	0·21	0·31	0·27	3–2	3–2	3–2	0–0
5.	2·80	0·86	1·05	0·57	0·81	0·43	0·20	0·30	0·26	3–2	2–4	2–3	0–0

Data for measured specimens: 1, *Taraxacum*, Fort Collins, Colorado, U.S.A., 6/vii/32; 2–5, *Taraxacum* sp., Wageningen, Holland, x/39. (*All leg. H. R. L.*)

Host Plants.

Known for certain only from *Taraxacum*, but recorded by Mordwilko (1935) from related genera.

Biology.

Attempts to transfer *rara* from *Taraxacum* to *Sonchus asper*, *Cirsium arvensis* and *Centaurea scabiosa* were not successful, although individuals would live for a long time on *Sonchus*. This aphid has only been found with *Lasius flavus* or *L. umbratus*. Mordwilko (1935) records *Helianthus*, *Cichorium* and *Centaurea*, in addition to *Taraxacum*, as hosts of *rara*.

Geographical Distribution.

Trama rara is recorded from North America (Colorado) as *T. oculata* (by Gillette and Palmer), Japan and Russia (Mordwilko), and has been seen from Czechoslovakia (*leg. Dr. V. Pasek*), Holland (*leg. H. R. L.*) and England. In England it has been seen from Wheathamsted (*leg. Mr. A. H. Strickland*) and Harpenden (Theobald collection), Herts., and has been found at the latter and in Reading, Berks. (recorded as *Trama oculata* Eastop, 1951).

Notes.

American material of *oculata* has been compared with European material from Czechoslovakia, Holland and England, and no significant differences could be found. Mordwilko himself thought that *oculata* was a synonym of *rara*, as is stated by Gillette and Palmer (1931). The paper in which *T. rara* was originally described has not been seen, but Mordwilko (1935) refers to this species as *T. rara* Mordwilko, 1908. Buckton (1881), pl. cii, fig. 5, shows a normal aptera of *T. troglodytes* and a newly ecdysed adult which has the hind tarsus/tibia ratio of *Trama rara*.

Trama troglodytes Heyden, 1837 (sensu latiore).

1837, Heyden, C. H. G. von, *Trama troglodytes* ; 1856, Koch, C. L., *Trama radicis* and *Trama pubescens* ; 1881, Buckton, G. B., *Trama troglodytes*, partim ; 1915, Goot, P. van der, *Trama pubescens* ; 1929, Theobald, F. V., *Trama troglodytes*, partim (apterae) ; 1930, Gillette, G. P., and Palmer, M. A., *Trama troglodytes* ; 1931, Gillette, G. P., and Palmer, M. A., *Trama troglodytes* ; 1932, Börner, C., *Trama troglodytes* ; 1935, Mordwilko, A., *Trama troglodytes* and ? *T. rara*, partim ; 1940, Börner, C., *Trama voigti*, *T. centaureae* and *T. mordwilkoi* ; 1942, Oestlund, O. W., *Trama troglodytes* ; 1948, Mordwilko, A., *Trama troglodytes* and ? *T. rara*, partim ; 1952, Börner, C., *Trama troglodytes*, *T. centaureae*, *T. mordwilkoi*, *T. pubescens*, *T. longitarsus*.

Morphology.

Apterae.—Eyes of three facets in true apterae and hind tarsus/hind tibia ratio = 0·70–0·82. Alatiform apterae with eyes of many facets, often ten to twenty and sometimes more, and hind tarsus/hind tibia ratio = 0·65–0·78. Hind tibia/III antennal segment ratio = 2·45–3·00. Most other characters very variable as this is almost certainly a complex of many species or sub-species.

Measurements of apterae.

	Body length.	Hind tarsus.	Hind tibia.	Mid femur.	Ultimate rostral segment.	Length of antennal segments.				Rhinaria on antennal segments.			
						III.	IV.	V.	VI.	III.	IV.	V.	VI.
1.	3·78	0·79	1·08	0·59	0·26	0·41	0·18	0·33	0·28	0	0	0–0	0
2.	3·53	0·87	1·22	0·68	0·29	0·44	0·21	0·39	0·31	0	0	1–0	0
3.	3·25	0·98	1·36	0·70	0·30	0·49	0·26	0·40	0·33	0	0	0–1	0
4.	3·10	0·92	1·38	0·70	0·28	0·54	0·28	0·44	0·31	0	0	0–0	0
5.	3·05	0·79	1·20	0·64	0·24	0·46	0·21	0·36	0·28	0	0	0–0	0

Data for measured specimens : 1, *Taraxacum*, Harpenden, Herts., 8/ix/48 ; 2, *Sonchus asper*, Horndon on the Hill, Essex, 6/vii/48 ; 3, *Cirsium arvensis*, Cambridge, 28/ix/51 ; 4, *Centaurea nigra*, Fulbourne, Cambs., 15/x/50 ; 5, *Doronicum* sp., Reading, Berks., 11/v/49 (*leg. Dr. F. H. Gravely*).

Alatae.—Eyes large and of many facets. Hind tarsus/hind tibia ratio = 0·60–0·73. Secondary rhinaria on antennae : III, 0–4 ; IV, 0–4 ; V, 0–6 ; VI, 0–1.

Measurements of alatae.

	Body length.	Hind tarsus.	Hind tibia.	Mid femur.	Mid tibia.	Length of antennal segments.				Rhinaria on antennal segments.			
						III.	IV.	V.	IV.	III.	IV.	V.	VI.
1.	3·28	0·82	1·33	0·67	1·08	0·56	0·23	0·35	0·30	4–4	3–3	2–3	0–0
2.	3·21	0·81	1·25	0·64	1·03	0·48	0·21	0·33	0·28	0–0	1–0	2–3	0–0
3.	3·09	1·00	1·39	0·70	1·00	0·55	0·26	0·42	0·34	0–0	0–1	2–1	0–0
4.	3·05	0·97	1·38	0·68	0·97	0·56	0·25	0·42	0·32	0–0	0–0	2–1	0–1
5.	3·73	0·96	1·42	0·73	1·03	0·55	0·26	0·42	0·31	1–1	3–3	6–3	0–0
6.	3·91	0·94	1·38	0·71	1·01	0·59	0·24	0·41	0·30	2–4	1–2	5–3	0–0

Data for measured specimens : 1 and 2, *Taraxacum*, Roermond, Holland, 11/vi/30 (*leg. H. R. L.*) ; 3 and 4, *Sonchus* sp. Wheathamsted, Herts., 9/x/51 (*leg. Mr. A. H. Strickland*) ; 5 and 6, *Cirsium arvensis*, Reading, Berks., 1/vi/48.

Host Plants.

Trama troglodytes has been recorded from many Compositae and material has been seen from the following: *Aster* sp., *Helianthus* sp., *Achillea millefolium*, *Chrysanthemum maximum*, *Artemisia vulgaris*, *Doronicum* sp., *Arctium lappa*, *Cirsium arvensis*, *C. lanceolata*, *Centaurea nigra*, *Cynara scolymus*, *Cichorium endiva*, *Hypochoeris radicata*, *Lapsana communis*, *Leontodon* sp., *Picris* (*Helminthia*) *echioides*, *Sonchus asper*, *S. oleraceus*, *Taraxacum officinale.*

Biology and Notes.

The unit here recognized as the species *troglodytes* is with very little doubt a complex of species, sub-species or races. In a group with no known sexual reproduction it is even more difficult than usual to differentiate between such terms. Some groups of the complex have fairly constant characters and may be separated from other " species," if not absolutely, at least by a comparison of means and often at very high levels of significance for several characters. Colonies from a few plants vary greatly, without any bimodality suggesting more than one species. There seems little doubt that a number of the " species " live on different hosts at different seasons of the year. Thus all the colonies collected from *Achillea millefolium* fall into one of two well-marked groups, absolutely separable from each other by a number of characters. One of these groups may be found on *Achillea* all the year round and the other only in the spring and early summer. About sixty transference experiments were attempted with members of the *troglodytes* complex, and only nine of these were definitely successful. All the successful experiments with one exception (*Sonchus oleraceus* to *Crepis* sp. in July) occurred in October, November or December. In a number of cases attempts to make the same transfers in midsummer were unsuccessful. The successful experiments were: *Taraxacum* to *Sonchus asper* and *Lapsana communis*, *Sonchus* spp. *to Taraxacum* (twice) and to *Crepis* sp., and four out of six attempts were successful from *Cirsium arvensis* to *Artemisia vulgaris*. The above results may not be entirely due to host-plant specificity as the biological form of aphid most likely to transfer in nature is the alata and in all experiments only apterae were used, as too few alatae were found in the field or reared in the laboratory at any one time to enable comparable experiments to be undertaken. The transference experiments suggest that during the summer members of the *troglodytes* complex do not readily leave their host but that they do so more readily in the autumn.

A number of colonies were compared with each other by comparison of means tests of those characters which seemed to show the greatest separation; more than one-third (422 out of 1140) of these tests showed significant differences at the generally accepted level, and these differences are not so arranged to separate the complex into a number of different groups.

Names that have been used in the troglodytes *Complex.*

Trama troglodytes Heyden, 1837: The original description leaves no doubt as to its generic position but further than that the description is of little use. The host plant is not given, and the only clue to the application of the name is that it was found with the ant, *Formica caespitum*. Thus, should this complex be separated in the future, it will be difficult to decide to which species the name *troglodytes* should be applied.

Trama pubescens Koch, 1856: This species was described from *Achillea millefolium* and is not necessarily distinct from *troglodytes*. Koch says that *pubescens* is scarcely distinguishable from *radicis*, but this is based on a misapplication of the name *radicis*. There appear to be two morphologically separable species on *Achillea millefolium*, but as neither of them are completely separable from all the colonies from other plants, no attempt has been made to decide to which the name *pubescens* should be applied. In the absence of other evidence it is more reasonable to apply the name to species staying on the plant all the year which is characterised as follows : Mid femur/ultimate rostral segment ratio varying from 2·2–2·5, mean 2·4 ; III antennal segment/VI a.s. = 1·3–1·5, m. 1·4 ; III a.s./V a.s. ratio = 1·0–1·2, m. 1·1 ; V a.s./IV a.s. ratio = 1·6–1·9, m. 1·7. The other species is characterised by : Mid femur/u.r.s. ratio = 2·5–2·7, m. 2·6 ; III a.s./VI a.s. = 1·5–1·7, m. 1·6 ; III a.s./V a.s. ratio = 1·2–1·4, m. 1·3 ; V a.s./IV a.s. = 1·3–1·6, m. 1·5. Van der Goot (1915) uses the name *pubescens*, but that is because he thought that the name *troglodytes* applied to a species with siphunculi.

Trama centaureae Börner, 1940, is described as differing from *troglodytes* by having a short-based mid-thoracic furca and an undivided head in the apterae, and in feeding on *Centaurea scabiosa*. No material of *Trama* has been found on *C. scabiosa* by the author and no material from other hosts could be transferred to it. The morphological characters given for *centaureae* do not, however, separate it from all other *Trama* spp. It has been shown above that the distinctness of the suture of the frons varies with the degree of alatiformity and that truly apterous Tramini do not have a suture. The mid-thoracic furca is also very variable in material from some plants, particularly from *Cirsium* and *Sonchus*, where a single colony may contain all the known variation in this structure. In the autumn of 1950 two colonies of *Trama* were found on *Centaurea nigra*, some specimens of which had a very faint median suture of the head and all of them had a short-based mid-thoracic furca. Transference experiments were not tried with this material and no further discoveries of *Trama* on *Centaurea* could be made.

Trama voigti Börner, 1940, is said to differ from *Trama pubescens* by the short-based mid-thoracic furca and in the hind tarsus being always shorter than the mid femur, and by feeding on *Doronicum*. This description again fits the very small amount of material seen from *Doronicum*, but does not separate it from material from all other plants. In 1952 Börner places *voigti* as a synonym of *T. longitarsus* (Ferrari), but this is not thought to be correct, as Ferrari describes the siphunculi of his *Lachnus longitarsus*, and would not have placed the species in *Lachnus* had siphunculi been absent.

Trama mordwilkoi Börner, 1940, is given as a nom. nov. pro *Trama troglodytes* Mordwilko nec Heyden, without further explanation. Mordwilko described the head of the aptera of *troglodytes* as being undivided, and as Börner's conception of *troglodytes* has a divided head (see original description of *T. centaureae*, Börner, 1940), this is thought to be the reason a new name was proposed. Mordwilko lists *Achillea*, *Artemisia*, *Sonchus* and other composites as hosts of his *troglodytes*, and Börner (1952) lists *Sonchus* (*asper* and *oleraceus*), *Crepis virens*, and states that it also occurs on *Cirsium arvense* and

Arctium lappa, adding that it is very common. It is thought that Mordwilko was describing the true apterae of a number of species, and thus *mordwilkoi* will be another name difficult to apply when the group is fully worked out.

Geographical Distribution.

T. troglodytes is recorded from Siberia (Mordwilko), Finland (Heikinheimo, 1948), Germany (Heyden, 1837, Koch, 1856, as *pubescens* and *radicis*) and material has been seen from Switzerland (*leg. H. R. L.*) and Britain. In Britain members of this complex have been seen from Kent (Theobald collection, B.M.), Essex, Berks., Herts., Cambridge, Somerset and Anglesey (Thomas and Jacob, 1940).

SPECIES NOT SEEN.

Trama antennata Mordwilko, 1931 : This species was described from *Rumex* in Turkestan and has not subsequently been recorded. It is thought that *Tactilotrama* Börner, 1950, of which *antennata* is the type species, is best regarded as a sub-genus of *Neotrama*, as is discussed in that genus.

Longitarsus taraxaci Shinji, 1932 : The paper in which the species was described has not been seen. Monzen (*in* Takahashi, 1938), according to Börner, 1952, places *Longitarsus* as a synonym of *Neotrama.*

Pemphigus auriculae (Murray, 1877), *Prociphilus erigeronensis* (Thomas, 1879), *Tychea radicicola* Oestlund, 1886, and *Aphis radicum* Fonsc., 1841, are names that have been used in the Tramini subsequently to their original description. It is not thought that any of these names apply to members of the Tramini as here understood.

HOST PLANT LIST FOR THE TRAMINI.

Because of the confusion in the host plant records of Tramini, the only hosts listed here are those from which the author has seen material (see list at top of next page).

DISCUSSION.

The three major difficulties in the present work are those of the species concept in a group in which sexual reproduction does not occur, the statistical level of significance to be accepted when dealing with animals which are parthenogenetic and the practical problem of the great dependence of some aphids on ants. As far as the species concept is concerned the greatest need is for a knowledge of the mutation rate of heritable characters in parthenogenetic reproduction. If the rate is low it should be possible to work out a system of names with some biological meaning for such complexes as that of *Trama troglodytes*, by means of biological and serological methods ; if the mutation rate is very high this may not be practicable.

The usual method of statistically investigating taxonomic problems for interbreeding animals is to calculate " comparisons of means " of the different populations. A large difference and significant result between two populations means, mathematically, that the variation within each population is small compared with the difference between the means of the populations, and thus it is unlikely that the two samples were drawn from the same population.

COMPOSITAE.

Asteroideae. *Aster* sp.	*Trama troglodytes.*
Helianthoideae. *Helianthus* sp.	*T. troglodytes.*
Anthemideae. *Achillea millefolium*	*T. troglodytes.*
Artemisia annua	*Protrama flavescens.*
,, *campestris*	*P. longitarsus.*
,, *vulgaris*	*P. flavescens* and *T. troglodytes.*
Chrysanthemum maximum	*Trama troglodytes.*
,, sp. cultivated	*P. flavescens.*
Senecionideae. *Doronicum* sp.	*T. troglodytes* (*voigti*).
Cynareae. *Arctium lappa*	*T. troglodytes* and *P. radicis.*
Carduus marianus	*P. radicis.*
Cirsium arvensis	*P. radicis* and *T. troglodytes.*
,, *lanceolata*	*T. troglodytes.*
Centaurea nigra	*T. troglodytes.*
,, *scabiosa*	*P. radicis.*
Cynara scolymus	*P. radicis* and *T. troglodytes.*
Cichoraceae. *Cichorium endiva*	*T. troglodytes* and *N. caudata.*
Hypochoeris radicata	*T. troglodytes* and *N. caudata.*
Lapsana communis	*T. troglodytes.*
Leontodon hastilis	*T. troglodytes.*
Picris echioides	*T. troglodytes* and *N. caudata.*
Sonchus asper	*T. troglodytes* and *N. caudata.*
,, *oleraceus*	*T. troglodytes* and *N. caudata.*
Taraxacum officinale	*T. rara, T. troglodytes, N. caudata.*

RANUNCULACEAE.

Ranunculus repens and *R. bulbosus*	*Protrama ranunculi.*

In interbreeding populations producing only one biological form, excepting sexual differences, a significant difference in a comparison of means is suggestive that the two samples belong to different species. As the genetical variation between the young of one parthenogenetically reproducing root-feeding aphid should be very small and as the environment of all the individuals feeding on the same root must be very similar, it is not surprising to find that there is very little morphological variation between members of the same generation of the same colony. When one colony is compared with another feeding on a different plant growing in a different place it is most probable that the two colonies will differ morphologically in some respects, and, as the variation within each colony is very small, they may be separated from each other statistically at a high level of significance. It has been observed in this *Trama* work that it has usually been possible to separate any colony collected in the field from all others so collected at what is usually accepted as a very high level of significance, often for a number of characters. It is also sometimes possible to separate successive generations of the same colony, this presumably being due to nutritional and other environmental effects. It is possible to select a much greater difference to be regarded as significant and this has been done. While this reduced the number of colonies that were significantly different from each other, it did not tend to arrange the colonies into groups corresponding with what, on biological grounds, are believed to be the distinct species, and the groups produced by the higher level of significance were certainly no nearer biological reality than those produced by the lower levels.

As all the variable and measurable characters observed were tested by these statistical methods, it would seem that one of the three following hypotheses must be correct: Firstly, that only one species is present which does not transfer readily from one host to another, and owing to its parthenogenetic reproduction, forms a series of colonies that may be separated from each other at very high levels of significance. It is thought that the biological work indicates that more than one species is present, that is if by species we mean the smallest natural group which is biologically distinct from its closest relatives because of its functional inability to interbreed with them. The second hypothesis is that more than one morphologically separable species is present, but that the comparison of means is not the correct method for their statistical separation. Whether or not this view is correct, there would seem to be a need for statistical as well as biological research in parthenogenetically reproducing populations.

The third hypothesis is that more than one species is present, but that they are not morphologically separable. Serological and other microchemical methods would seem to be one way of investigating these and other taxonomic problems. If there are biologically distinct but morphologically identical groups present there is a problem of nomenclature. Although it is possible and certainly most easy to regard all such groups as races of one species, this is neither necessarily correct nor most convenient, as if the insects are biologically distinct they must have names of some kind for the use of the plant pathologist, and a race or varietal name must be at least a trinomial.

If there was an original species with both sexual and asexually reproducing forms, as is most likely, and the sexual generation has been lost, leaving only the offspring of one sexually reproducing pair, all the specimens now in existence may reasonably be regarded as belonging to one species, which has split into a number of races feeding on different plants or having a different range of food plants. It is important that these races are regarded as races of the species which has lost its sexual generation and not the original sexually reproducing form. This is important, both practically and theoretically—practically because many aphids produce their sexuales on a primary host in the autumn and the parthenogenetic forms spend the summer on a secondary host. When the sexual generation is lost so, often, is the primary host, completely or considerably altering the economic importance of the aphid. The theoretical reason is that the ability to reproduce sexually must surely be a character of greater importance than many of those generally accepted for separating species. If many races were formed separately by loss of the sexual generation, as is much more probable, these races cannot all be regarded as belonging to the same species as they are only related to one another through another distinct (sexually reproducing) species. Each original split from the parent species should thus be regarded as a good species, only succeeding parthenogenetic mutation being regarded as having given rise to races.

It is most unlikely that any two splits from the original sexually reproducing species would have an identical genetical constitution, but it is possible, and thus it is also possible to have, in theory, two distinct, species with identical genetical constitutions. The term "species" should be a taxonomic aid and not a hindrance, and thus similar groups with a claim to be regarded as distinct species should only be given binominals when their biological differences justify it, and when there are reasonable methods available for applying the same name to the same species when it is refound. It is for this reason that binominals have not been given to a number of "species" in the *Trama troglodytes* complex in the present paper.

The dependence on ants presented a practical problem in the host transference experiments. It was found easier to take about a dozen ants from the nest where the aphids were found, and to replenish the supply in about ten days from the same nest, than it was to maintain a separate ant colony for each transference test. The following records of Tramini in ants' nests are thought to be correct; there are other records in which the identification of either the aphid or the ant is in doubt.

Formica fusca . .	*Protrama* sp.
,, *rufa* . . .	*Trama troglodytes.*
Lasius alienus . .	*Protrama* sp.
,, *flavus* . . .	*Trama troglodytes, T. rara, Protrama* sp.
,, *niger* . . .	*T. troglodytes, Neotrama caudata.*
,, *umbratus* . .	*T. troglodytes, N. caudata caudata* and *N. c. maritima.*
Myrmica scabrinodis .	*T. troglodytes.*
Tetramorium caespitum .	*T. troglodytes, Protrama flavescens.*

There was some apparent specificity between aphids and ants, but it could have been entirely due to certain ants, host plants and aphids favouring certain types of soil. Thus *Sonchus asper* growing as a weed of neglected cultivated ground is often infested with *Neotrama caudata* living in the nests of a yellow *Lasius.*

SUMMARY.

Characters have been given to separate the known genera of the Tramini. The British species have been keyed out where possible, and where not possible there has been a discussion of the complex concerned. Non-British species have been discussed in the section on species not seen by the author. An account has been given of the taxonomic problems encountered in a group whose only known method of reproduction is parthenogenetic.

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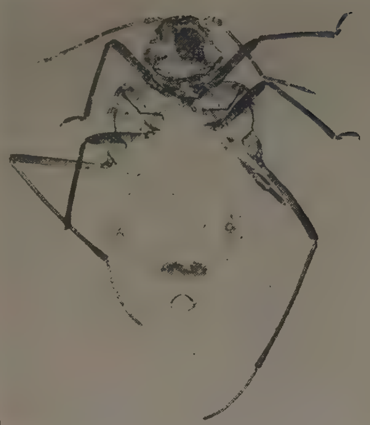
PLATE I.

Fig. 1.—*Protrama longitarsus* Ferrari, alatiform aptera.
Fig. 2.—*Protrama ranunculi* (Del Guercio), alatiform aptera.
Fig. 3.—*Neotrama caudata* subsp. *maritima*, aptera (type specimen).
Fig. 4.—*Neotrama caudata caudata* (Del Guercio), alata.
Fig. 5.—*Trama troglodytes*, aptera from *Centaurea nigra*.
Fig. 6.—*Trama troglodytes* Heyden, alata.



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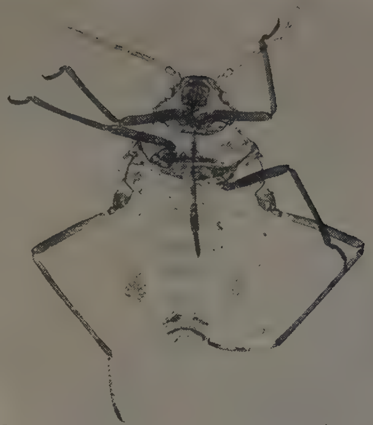

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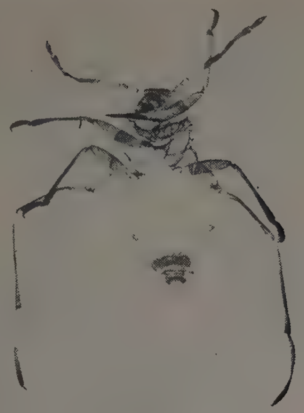

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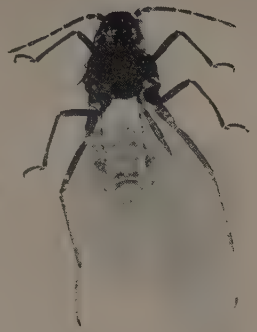

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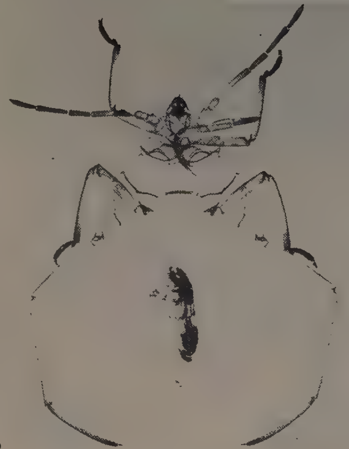

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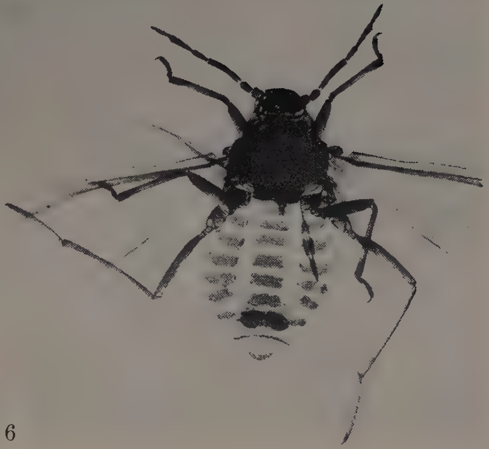

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V. F. Eastop.

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THE MORPHOLOGY AND TAXONOMY OF THE GENUS *ORTHOTYLUS* FIEBER (HEM., MIRIDAE), WITH SPECIAL REFERENCE TO THE BRITISH SPECIES.

By T. R. E. Southwood, B.Sc., A.R.C.S., F.R.E.S.

(Entomology Dept., Rothamsted Experimental Station, Harpenden.)

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(Read 6th May, 1953.)

With 152 Text-figures.

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1. Morphology.

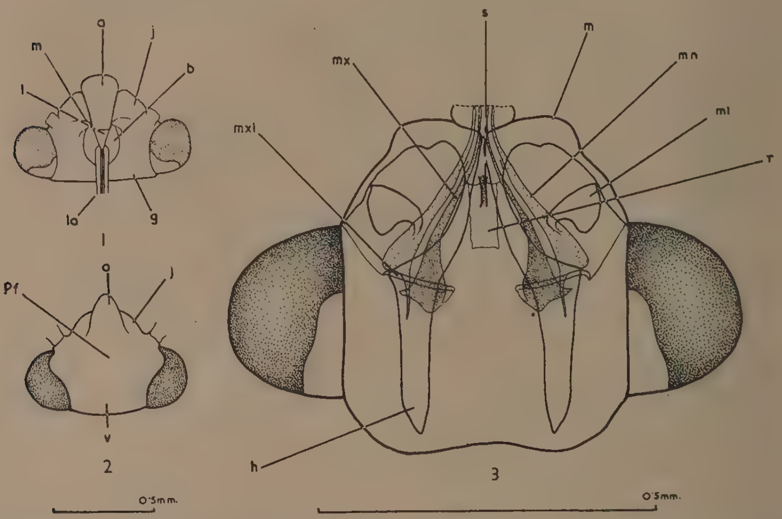
a. Method.

The specimens used in this part of the work had been preserved in 70 per cent. alcohol; dried pinned specimens were also frequently examined. The preserved material was boiled in 10 per cent. caustic potash and cleared either in creosote, cedarwood oil or clove oil. Structures were sometimes stained in 10 per cent. acid fuschin before clearing. Smaller structures were drawn when mounted in balsam, the larger ones (i.e., the thorax) when in the clearing agent, with the help of camera lucida or squared eyepiece and graph paper.

b. Head.

The head of *Orthotylus* is of the prognathous type and highly specialised to accommodate the sucking mouth parts and their associated muscles.

Head capsule.—The gular region, as in most Heteroptera, is well developed (fig. 1), completely fused with the genae, no trace of a gular suture being visible in the adult. The clypeus is greatly enlarged compared with the condition in the primitive insect, and is divided into the anteclypeus and the postclypeus (fig. 2); there is no suture between them, but the division is considered to occur where the clypeal folds (sometimes incorrectly referred to as "frontal sutures") end. The anteclypeus, the "tylus" of many authors, is very convex, but parallel sided.



Figs. 1–3.—*Orthotylus flavosparsus.* (1) Head, ventral view. (2) Head, dorsal view. (3) Head, ventral view; gular area removed to show internal structure. *a*, anteclypeus; *b*, buccula; *g*, gular area; *h*, hypopharyngeal wings; *j*, jugum; *l*, labrum; *la*, labium; *m*, maxillary plate; *ml*, mandibular lever; *mn*, mandibular stylet; *mx*, maxillary stylet; *mxl*, maxillary lever; *pf*, postclypeus + frons; *r*, food canal; *s*, salivary pump tendon; *v*, vertex.

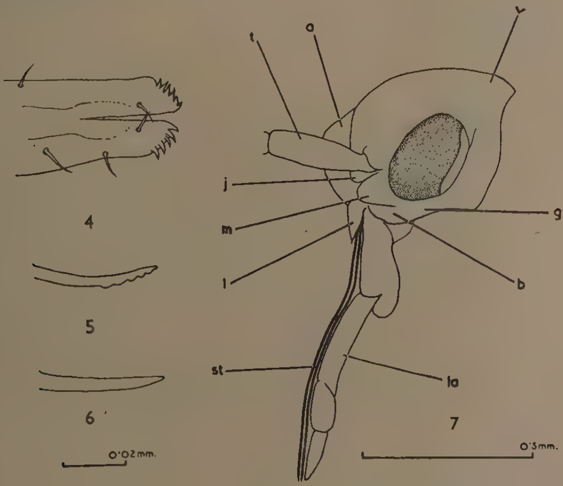
Lateral to the anteclypeus are two plates; Snodgrass (1935) refers to the more dorsal as the mandibular plate and the lower one as the maxillary plate (fig. 7). They are separated by what Muir and Kershaw (1911) call the mandibular suture (although in the legend of their illustrations it is referred to as the maxillary suture), which runs back to the base of the antennae.

The mandibular plate merges posteriorly with the fused postclypeus and frons, while the maxillary plate merges with the genae.

It is useful to list the various terms applied by different authors to these plates:

Authors.	*Mandibular plate.*	*Maxillary plate.*
Muir & Kershaw (1911).	Frontal ridge.	Maxillary plate.
Snodgrass (1935).	Mandibular plate.	,, ,,
Knight (1941).	Jugum.	Lorum.
Börner (1935).	Genae or cheek wings (Oberkieferlappen).	Galea or lorum (Unterkiefer-Stammstück).
Butt (1943).	Jugum.	Maxillary plate.
Spooner (1938).	Paraclypeus.	,, ,,
Macgill (1947).	Jugum.	,, ,,
Newcomer (1948).	,,	,, ,,

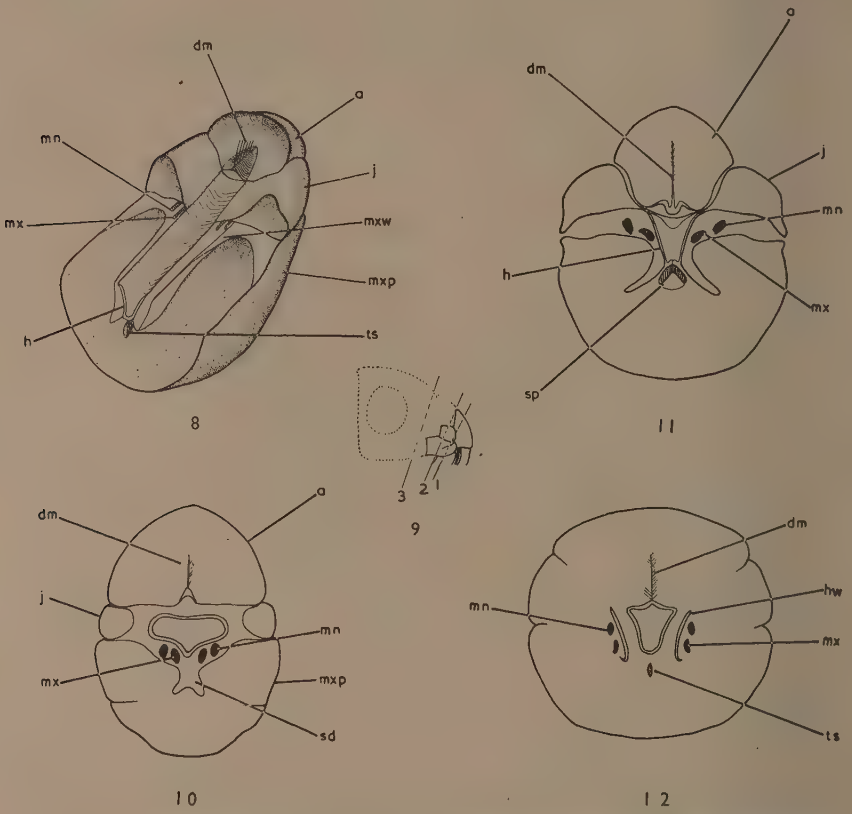
Matters are further confused, for in the Homoptera the mandibular plates are referred to as lora.



FIGS. 4–7.—*Orthotylus flavosparsus.* (4) Tip of labium. (5) Tip of mandibular stylet. (6) Tip of maxillary stylet. (7) Head, lateral view. *a*, anteclypeus; *b*, buccula; *g*, gena; *j*, jugum; *l*, labrum; *la*, labium; *m*, maxillary plate; *st*, stylets; *t*, antenno-basal joint; *v*, vertex.

The discrepancy in terminology is mainly due to varying opinions regarding the homologies of these plates, especially of the mandibular. In order to investigate the internal relationship of these plates to each other and to the mouth parts, it was necessary to use at first a somewhat larger Heteropteran than *Orthotylus*, and a species of *Dysdercus* was investigated.

Snodgrass (1938, 1950) has suggested that the lorum of Hemiptera arises from the hypopharynx, while Spooner (1938) and Evans (1938) maintain that it is a detached area of the postclypeus. Butt (1943) and Willis (1949) have shown conclusively that the lora of the Homoptera are directly attached to the hypopharynx. Butt suggests that, while the lora of Homoptera are horizontal plates, those of the Heteroptera are vertical, connecting the side wall of the hypopharynx and the mandibular plates or juga (which are the plates visible externally). However, Macgill (1947) does not show or suggest any connection between the hypopharynx and the mandibular plates of *Dysdercus* (figs. 8–11). The present work (based on dissections and hand sections of macerated material) has shown definitely that such a connection occurs, although only for a short distance.



Figs. 8–12.—*Dysdercus* sp. (8) Block diagram of anterior part of head, viewed posteriorly, to show arrangement of internal structures. (9) Diagram of head showing outline of fig. 8 (in heavy lines) and regions of sections figs. 10–12. (10) Section through region 1 of fig. 9. (11) Section through region 2 of fig. 9. (12) Section through region 3 of fig. 9. *a*, anteclypeus ; *dm*, " tendon " of dilator muscle of food pump ; *h*, hypopharynx ; *hw*, hypopharyngeal wings ; *j*, jugum ; *mn*, mandibular stylet ; *mx*, maxillary stylet ; *mxp*, maxillary plate ; *mxw*, maxillary wings ; *sd*, salivary canal ; *ts*, tendon of salivary pump.

The work of Newcomer (1948) on the embryology of *Oncopeltus* has shown that this complex of the vertical plate (lorum of Butt) and horizontal plate (jugum or mandibular plate) is also in origin a compound structure formed from the sides of the hypopharynx and from the clypeus. It is formed by the close proximity of these areas at blastokinesis, and the development and postembryonic elongation of the mandibular sutures (maxillary clefts of

Awati, 1914); the exact boundaries are impossible to define even in the adult. For morphological considerations, however, the author feels that Butt's terms are the most satisfactory (i.e., the external horizontal plate—Jugum, the internal vertical plate—Lorum).

Sutures are absent in the posterior region of the head capsule of the adult *Orthotylus* and there is no trace either of ocelli or tentorium. The actual boundaries of the frons, vertex and other sclerites cannot therefore be determined externally.

The labrum is attached to the morphologically anterior (topographically ventral) margin of the anteclypeus; it is narrow, triangular in shape, coming into the second of the three groups into which Spooner divides heteropterous labra. Its dorsal (anterior) surface is much crinkled, while the ventral surface has a shallow groove for the stylets.

Mouthparts.—The mandibles and maxillae are represented by a pair of stylets with associated levers (figs. 3, 4 and 5). The mandibular levers belong to Ekblom's (1926) first group.

Most accounts do not describe the passage of the stylets in the anterior region of the head: it is therefore dealt with here in more detail. Where the stylets emerge from the head they pass over the sclerotised median tips of the maxillary plates, which are called the maxillary processes; just posterior to this they lie in a groove between the lateral wall of the hypopharynx and the backward projection of the maxillary wings. Posteriorly, the former gives rise to the hypopharyngeal wings; the latter are here referred to as the maxillary wings. These then fuse ventrally with the hypopharyngeal wings so that the stylets are only ensheathed on their inner side.

The labium is modified into the rostrum; the arrangement of bristles at its tip (fig. 4) is often said to be specific, but it was found to be identical in *O. flavosparsus*, *O. marginalis* and *O. moncreaffi*.

Antennae.—These have four segments or joints, as in all Miridae, and are attached to a small pedicel, anterior to the eyes. The third and fourth segments, and in some species the apex of the second, have numerous crenulate rings visible under very high power (fig. 18). These are found in some aphids and probably many other groups; nothing appears to be known of their structure or function.

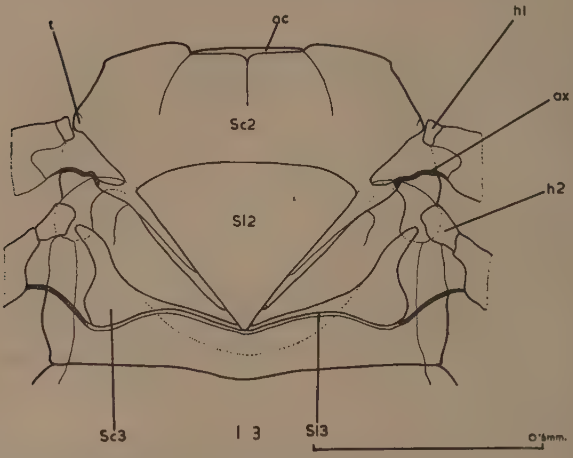
All four segments are thickly covered with hairs; in all species except *tenellus* these are of two distinct types (Table I). The short hairs are present on all segments, but the number and arrangement of the long hairs is of taxonomic importance.

c. Thorax.

The only works on the heteropterous thorax (though they make but scanty reference to the Miridae) are those of Taylor (1918) and Larsen (1943*a* and *b*); Brindley (1934) deals solely with the metasternum and pleuron.

There is a general tendency for the prothorax to overlap the mesothorax, while this overlaps the metathorax, reducing it especially in the notal region.

The pronotum is well developed and saddle-shaped; it continues back over the mesothorax almost to the scutellum. At the side the pronotum fuses with the epimeron (fig. 14), and continues ventrally posterior to the


t
ac
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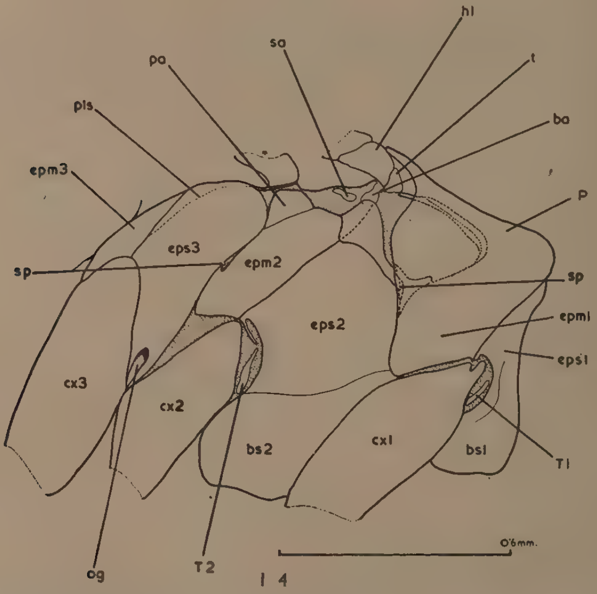
Sl2
h2
Sc3
13
Sl3
0·6mm.

FIG. 13.—*Orthotylus flavosparsus.* Dorsal view of meso- and meta-thorax. *ac*, acrotergite of mesothorax; *ax*, axillary chord; *hl*, humeral plate of front wing; *h2*, humeral plate of hind wing; *Sc2*, mesoscutum; *Sl3*, metascutellum; *t*, tegula.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cx1
bs2
bs1
T1
og
T2
14
0·6mm.

FIG. 14.—*Orthotylus flavosparsus.* Lateral view of thorax. *ba*, basalare; *bs1*, probasisternum; *bs2*, mesobasisternum; *cx1–cx3*, first to third coxa; *epm*, epimeron; *eps*, episternum; *hl*, humeral plate of front wing; *og*, odoriferous groove; *P*, pronotum; *Pa*, postalare; *pls*, pleural suture; *sa*, subalare; *sp*, spiracle; *T1 and T2*, first and second trochantins; *t*, tegula.

first coxal cavity as far as the mesoepisternum (fig. 15). The episternum is clearly visible anterior of the pleural suture; it fuses with the probasisternum, forming the wide precoxal bridge. The basisternum is terminated by a short spur and is followed posteriorly by the furcasternum.

In the mesothorax the acrotergite is visible at the extreme anterior margin of the segment (fig. 13), and can be identified by the first phragma which arises from it. The mesoscutum is large; closely adjoining its posterior margin is the scutellum, which extends backwards, covering most of the metanotum. The episternum is separated from the basisternum by a weak suture, while the pleural suture plainly separates it from the epimeron.

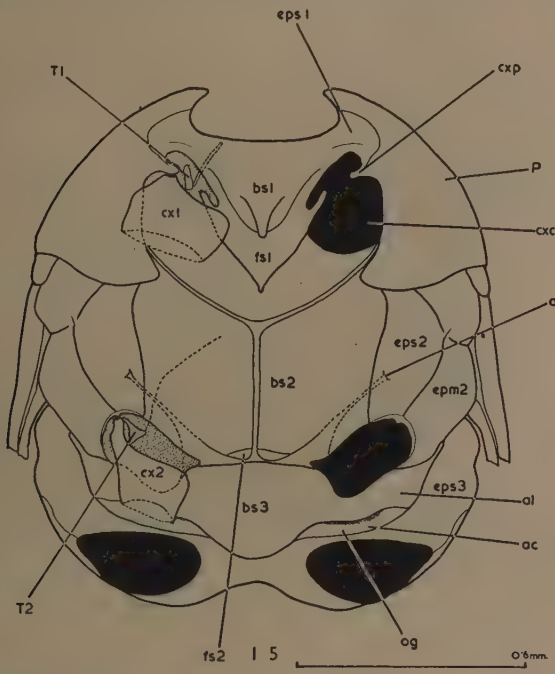
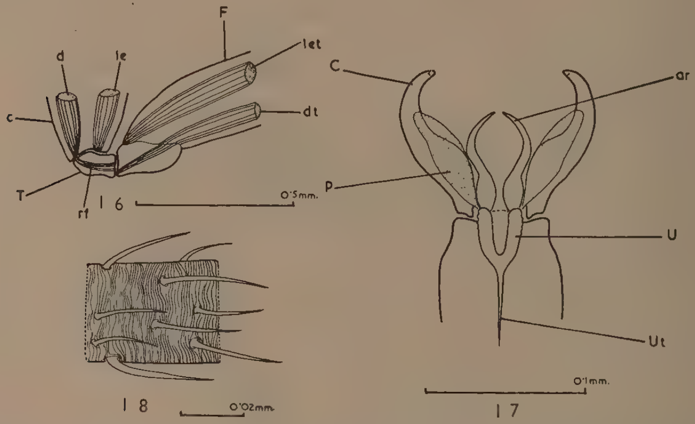


FIG. 15.—*Orthotylus flavosparsus.* Ventral view of thorax. *a*, apodeme; *ac*, antecoxal laterale; *al*, anterior laterale; *cxc*, coxal cavity; *cxp*, pleural coxal process; *fs*1, profurcasternum; *fs*2, mesofurcasternum. (Other abbreviations as in fig. 14.)

The metathorax is reduced and much modified; the scutum is narrow, but laterally enlarged and produced anteriorly to form the dorsal wing process. The scutellum is very narrow, and may be identified by the continuity of the axillary cord of the hind wing with its lateral extremities. The episternum is large and slightly overlaps the epimeron, which, together with the anterior position of the wing processes, causes the forward situation of the hind wing. This may lead to the misidentification of the intersegmental suture as the pleural suture. The precoxal bridge is wide and, according to Brindley (1934), consists of the antecoxal laterale and the anterior laterale, the suture between them being occupied by the odoriferous groove.

Legs.—Between the coxa and the " femur " are two " segments," and to determine the true homologies of these the musculature of this part of the leg was studied (fig. 16) by bleaching alcohol-preserved-specimens in diaphanol and then clearing. It could then be seen that the segment following the coxa contained only one muscle, the retractor of the femur. The second " segment " had one muscle which continued right through the ventral part of the femur proper and so must be considered the depressor of the tibia. This second " segment " must therefore be considered as the basal part of the femur. A similar condition is known in some Hymenoptera (Snodgrass, 1935).



Figs. 16–18.—*Orthotylus marginalis.* (16) Musculature of coxa, trochanter and base of femur. (17) Ventral view of tarsal and claw complex. *ar*, arolium; *C*, claw; *c*, coxa; *d*, depressor muscle of trochanter; *dt*, depressor muscle of tibia; *F*, femur; *le*, levator muscle of trochanter; *let*, levator muscle of tibia; *p*, pseudoarolium; *rf*, reductor muscle of femur; *T*, trochanter; *U*, ungitractor plate; *Ut*, " tendon " of depressor muscle of pretarsus (retractor of claws). (18) *O. flavosparsus.* Part of 4th antennal segment.

The tarsus is three-segmented; the apical segment (fig. 17) is the largest, bearing two claws and various other structures referred to by taxonomists as arolia and pseudoarolia (Knight, 1941; Carvalho and Leston 1952). Ventrally the unguitractor plate (Snodgrass, 1935), with the tendon of the depressor muscle of the pretarsus (retractor of claws), occupies a median position. Just anterior to this are the two arolia, while ventral to the claws are two flap-like membranous pads, the pseudoarolia; these seem to correspond with the pulvilli, although no auxilla could be seen.

The outgrowths of the integument variously described as " hairs," " spines," " spurs," etc., are of taxonomic importance and are really of four types:

(1) *Long hairs:* found only on the underside of the front femur of *O. viridinervis* and *O. diaphanus.*

(2) *Medium hairs :* found on the tibia of all species and often on the apex of the femur. They are somewhat thicker in proportion to their length than the other two types of hair.

(3) *Short hairs :* found all over the legs of all species.

(4) *Teeth :* these are stout black-tipped projections in four rows on the hind tibia of all species. They are about 0·001 mm. in length.

The length of the various hairs in different species is given in Table I. There is some intergradation between medium and short hairs, especially at the apex of the tibia.

TABLE I.—*Hair Length of various* Orthotylus *spp.*

	Antennae.		Legs.			Hemielytra.	
Species.	Long.	Short.	Long.	Medium.	Short.	Erect straight.	Adpressed curled.
fuscescens	95	50	—	95	55	110	85
tenellus	—	45	—	55	40	65	—
viridinervis	135	70	155	100	70	105	—
marginalis	130	65	—	100	65	140	—
ochrotrichus	95	45	—	70	45	115	—
ericetorum	85	55	—	105	50	115	—
adenocarpi	90	55	—	90	45	125	65
virescens	95	55	—	75	45	95	50
flavosparsus	90	45	—	70	45	95	50
moncreaffi	90	45	—	75	45	95	50
diaphanus	95	45	135	100	45	95	70

All measurements are in μ (a thousandth of a mm.) and are given to the nearest 5 μ, a blank indicates that the particular type of hair is absent in that species.

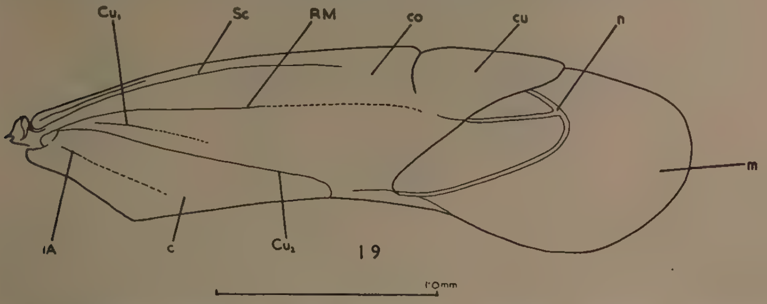


FIG. 19.—*Orthotylus flavosparsus.* Right hemielytra. *c*, clavus ; *co*, corium ; *cu*, cuneus ; *m*, membrane ; *n*, cell nervatures.

Wings.—The fore wings are modified into hemielytra, characteristic of the Heteroptera. An account of the structure of these is given by China and Myers (1929) ; the present study supported their system (fig. 19). The membrane of the male is often comparatively longer than that of the female. The hemielytra are covered with hairs of two sorts (see Carvalho and Leston, 1952).

(1) *Erect, straight hairs :* these are also longer and may be white or black.

(2) *Adpressed, curled hairs:* these are scale-like and easily rubbed off. They are black in *O. diaphanus*, but white in the other British species in which they occur.

The length of these hairs in various species is given in Table I and their arrangement discussed on page 437.

The membraneous hind wings have been studied in the Heteroptera by Tanaka (1926) and Hoke (1926), whose accounts differ; the present study supports the former. However, a more comparative study of the tracheation and development is necessary before any definite conclusions on venation can be reached.

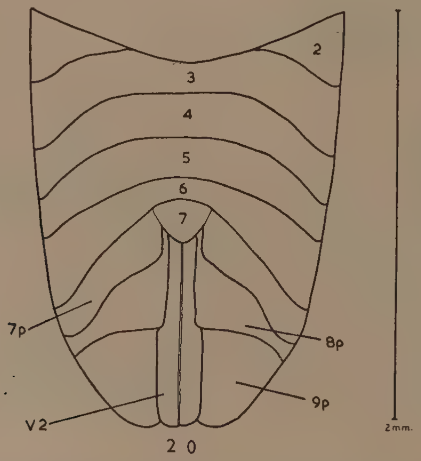


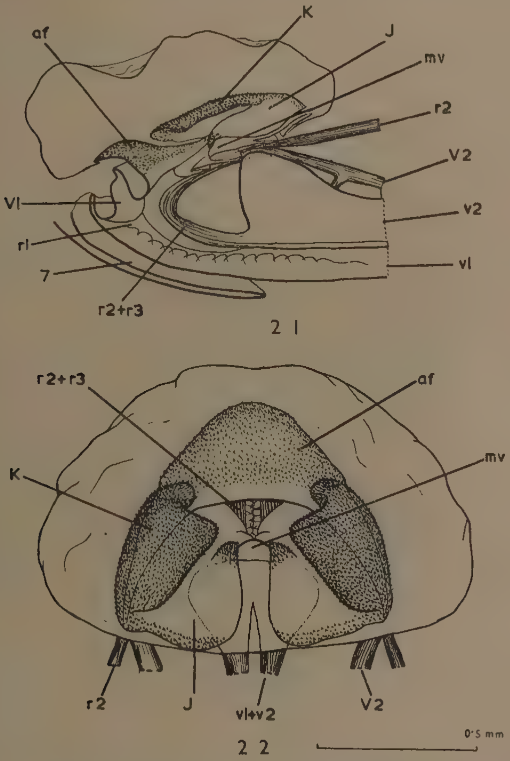
Fig. 20.—*Orthotylus flavosparsus*. Ventral view of female abdomen. *V*2, second valvifers; 2–7, second to seventh sternite; 7*p*–9*p*, seventh to ninth pleurite.

d. Abdomen.

Female.

Anterior to the genital segments, five sternites are visible ventrally; they represent segments 2 to 6 (fig. 20). The seventh sternite is triangular and forms the sub-genital plate (squamae of Wagner, 1942), which covers the base of the valvulae. The pleurites of the seventh, eighth and ninth segments extend to a ventral position lateral to the second valvifers. The anal cone occupies a dorsal and posterior position, and it is said to represent segments 10 to 11 (Snodgrass, 1935).

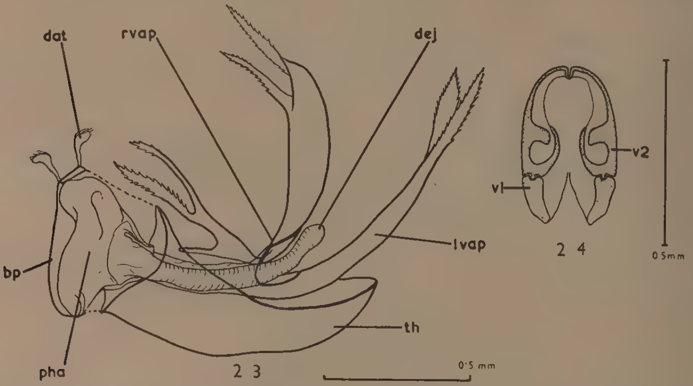
The various structures constituting the genital apparatus are derived from segments 8 and 9. There are two pairs of ovipositor blades (the valvulae), pointed with minute teeth; the dorsal valvulae have a peg on their lower edge, which fits into a groove on the upper edge of the ventral one (fig. 24). The ventral or first valvulae arise from a more anterior position and are considered to be derived from segment 8. Two rami arise from their anterior end and, according to Snodgrass (1933), the morphologically outer rami are attached to a flap of sclerotised material, the first valvifers (fig. 21). However, it appears that in *Orthotylus* these rami are somewhat displaced. From the first valvifers arise what are here termed the first rami, as they are the most anterior. These are short and join the ventral margin of the first valvulae on the median side as membranes; sometimes, as in *O. marginalis*, their edges are produced into finger-like outgrowths. The second rami also arise at the anterior end of the first valvulae but from their dorsal margin; these rami curve upwards, posterior to the first, and are continued as two rods to the anterior ventral angle of tergum 9. Slater (1950) calls these "connecting pieces," but these and the second rami appear to be a single structure and are referred to here by the latter name. They are the fibulae of Verhoeff (1893) and Kullenberg (1947) or the shanks of Ekblom (1926).



FIGS. 21, 22.—*Orthotylus marginalis.* (21) Longitudinal half of bursa copulatrix and associated structures. (22) Dorsal view of bursa copulatrix and associated structures (dorsal wall of b.c. removed). *af*, anterior fold; *J*, J structure; *K*, K structure; *mv*, membrane of ventral wall of b.c.; *r1–r3*, first-third rami; *V1 and V2*, first and second valvifers; *v1 and v2*, first and second valvulae; 7, seventh sternite.

The dorsal and more posterior pair of ovipositor blades, the second valvulae, are derived from segment 9. Attached to their anterior end are short rami (third rami), which bend steeply upwards and back, but closely adpressed and posterior to the second rami; they join two oblong plates which sheath the ovipositor when it is in resting position. These plates are the second valvifers of Snodgrass (1933) or the ovipositor sheath of Kullenberg (1946), and have a rod from their dorsal margin running obliquely ventrally almost to the ventral margin. Attached to the posterior end of the second valvifers are the third valvulae, which are short and ensheath the tips of the second valvulae.

The female gonopore, between the eighth and ninth segments, opens into a large pouch, the bursa copulatrix; the oviducts enter this dorsally. Slater (1950) described some of the sclerotised parts of the bursa copulatrix and reviewed their structure in the Miridae. Anteriorly where it is attached to the first valvifer (fig. 21) it is crescentic (from above), strongly curved and sclerotised with numerous short spines, and is here called the anterior fold (fig. 22). Its lateral arms are continued posteriorly on either side of the gonopore to the points where the two sclerotised flaps (K structures, Slater (1950)) are attached. These have a flange projecting ventrally and running along the outer margin, and are attached where the lateral arms of the anterior folds join ventrally with sclerotised areas of the floor of the bursa copulatrix (J structures, Slater (1950)). The tips and anterior margin of these, like the K structures, are covered with fine spines. Ventrally to the J structures the wall is mostly membraneous with numerous invaginations, which no doubt expand to allow the eggs to pass at the oviposition. The rest of the wall of the bursa copulatrix is membraneous in *Orthotylus*, except for two indistinct sclerotised areas on the anterior wall.



Figs. 23, 24.—(23) *O. marginalis*, Lateral view aedaegus. (24) *Orthotylus ochrotrichus*. T.S. ovipositor, anterior region. *bp*, basal plate; *dat*, dorsal attachment or connective (= capitate process); *dej*, ejaculatory duct; *lvap*, left vesical appendage; *pha*, phallosome; *rvap*, right vesical appendage; *th*, theca; *v*1 *and v*2, 1st and 2nd valvulae.

Male.

There are three views of the homologies of the male genitalia in the Hemiptera, viz., those of Snodgrass (1935 and 1936), Qadri (1949) and Marks (1951).

From the taxonomic angle the works of Kullenberg (1941*a*, 1947) and Singh Pruthi (1925) are very thorough, and the latter is followed in this study. Baker (1931) gives a detailed account of this structure in several Pentatomidae.

The structure of the male genitalia may be summarised :

(1) A pair of parameres, or claspers (figs. 26–33) ; Snodgrass calls them harpagones ; Marks (following Mitchener, 1944) calls them gonoforceps, and maintains they represent the fused coxite (and probably style) of segment 9 ; Qadri applies the term paramere to part of the aedeagus itself.

(2) The aedeagus or penis, which is much telescoped when at rest, consists of the basal membraneous phallosome arising from the theca (fig. 23) and the distal endosome with the gonopore at the tip. Normally from the membrane of the endosome arise two sclerotised appendages, the vesical appendages. The right appendage is slightly dorsal, and in some species (e.g., *marginalis*) has an anterior basal branch, so that there appear to be three appendages. The left appendage is slightly ventral ; both appendages are much branched and toothed in some species.

2. Taxonomy.

a. Technique.

Measurements.

All measurements were made from a directly dorsal aspect (except length of head, see below) with a squared or graduated eyepiece. Five males and five females (usually from different localities) of each species were measured. In *O. ochrotrichus*, however, 35 specimens were measured, but the average values were found only to differ from those of five specimens by a few hundredths of a millimetre, and it is considered that errors of measurement are probably greater than this ; for this reason also the lengths are given only to the nearest 0·05 mm. The total length was measured from the front of the head or the posterior (or dorsal) margin of the tylus (fig. 7) (junction of the anteclypeus with the postclypeus), when this was visible, to the apex of the membrane.

Measurements of the head length were made diagonally from the posterior margin of the vertex (apex of carina when present) to the morphologically anterior margin of the tylus, where this abuts the labrum. In this way there is no error due to the angle at which the head is mounted. The length of the cornified part of the hemielytra was taken from the apex of the humeral plate to the apex of the cuneus, and its breadth (not always the maximum) at right angles across from the tip of the scutellum, when the wings are in their normal resting position.

Hairs.

The various types of hairs on the antennae, femur and hemielytra are described on page 423 (Table I). Many of these are easily rubbed off.

Colour.

Dead *Orthotylus* lose their natural green colour, but Massee (1949) described a method of treatment with formalin vapour which keeps the colours very close to those during life.

In specimens so treated no difficulty will be experienced with colours of the cell nervures, but in faded specimens these colours should be compared with those of the cuneus.

Genitalia.

Enough of the claspers may usually be seen from the terminal view of the male genital capsule *in situ.* For a more detailed examination of dried specimens the abdomen must be removed and softened (*not* macerated) in warm dilute caustic potash solution (2 per cent.) *for a short time*, and the claspers removed to 70 per cent. alcohol with fine-pointed forceps. If the specimen is not teneral they can be mounted with gum tragacanth on the card behind the specimen. In fresh specimens they can be removed without the use of caustic potash or alcohol. The claspers must be mounted so that they may be examined from various angles.

To examine the vesical appendages of the aedeagus or the structures of the bursa copulatrix, the abdomen must be gently removed, macerated in hot 10 per cent. caustic potash solution, and in this solution the genital region separated from the rest of the abdomen. There are various neutralizing, dehydrating and clearing methods; glacial acetic acid, absolute alcohol and cedarwood oil were commonly used in this work. The final dissection is usually done in the cedarwood oil, but it is advisable with the smallest species to do this in the mountant itself.

The K structures of the bursa copulatrix are best found by dissecting from the dorsal aspect. The dorsal wall should be split and pulled apart with forceps and then the K structures can be seen overlying its "floor" just above the third rami (fig. 22).

Finally the structures are mounted in naphthrax (preferable to balsam for its higher refractive index) or other mountant on a small strip of cellulose acetate with $\frac{3}{8}$-in. or smaller cover glass; this can then be pinned below the specimen.

b. Orthotylus scotti Reuter.

Douglas and Scott (1865) describe *Litosoma viridinervis* from specimens taken in the London district and "abundantly on plum trees at Darenth." Saunders, who had seen these specimens, sent Reuter (1877) one female from his own collection which Saunders considered to be the same species. Reuter realised that it was not *O. viridinervis* of Kirschbaum (1856), and described it as a new species, *O. scotti*, the chief characters being "the fourth joint not longer than the basal" and "the apical not nearly half as long as the third."

Reuter's description is confused, stating that "first joint three-fourths as long as the second," which is obviously false; also "vertex not marginate posteriorly," while the key gives the reverse. In his *Hemiptera Gymnocerata Europae* (1878) Reuter describes the characters of the male of *scotti* and gives figures of the claspers; this account is followed by Saunders (1892). Supposedly it differs from *prasinus* mainly in the right clasper, but it has been found that owing to its shape its appearance depends on the angle from which it is seen. It was impossible to separate the species on this character. Reuter says that the relative lengths of various segments of the antennae will distinguish the female, but, as Johnson (1939) has shown with *Cimex*, the use of small differences in the ratios of a structure so much affected by differential growth rate of the whole animal is unreliable; also in slightly teneral specimens the apical joint is often shrivelled and shrunk. However, the length of the various antennal segments of specimens determined by their K structures as *prasinus*, and of all those in both the Power and Butler Collections at the British Museum (Natural History), were measured; the ratios that, according to Reuter, separate the species were then calculated. Fig. 25 shows that these ratios are not segregated into distinct groups but form a continuous series. Dr. H. Lindberg of the Helsinki Museum kindly sent me the type of *scotti* (a female),

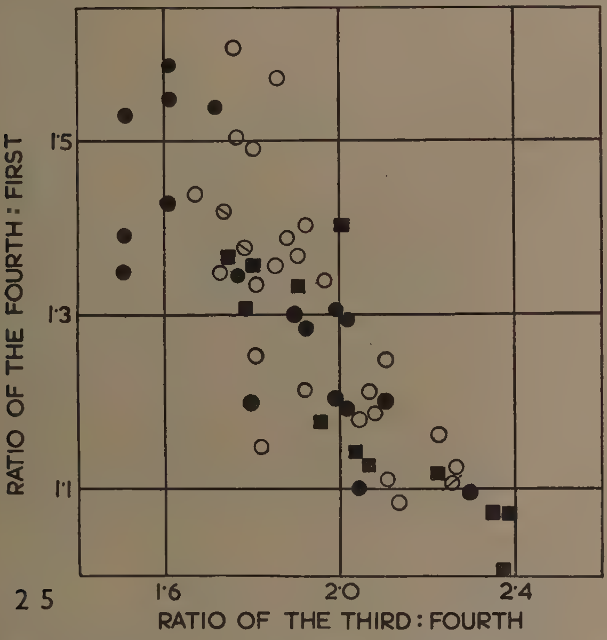


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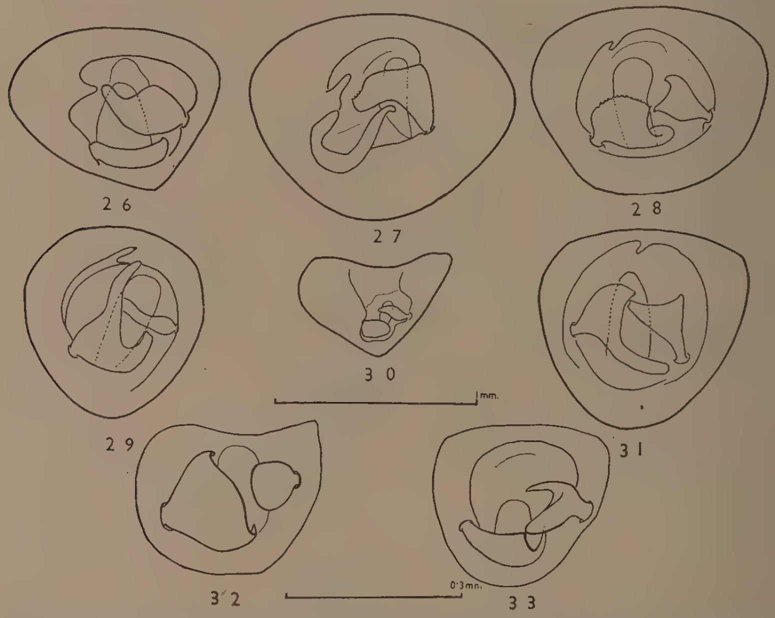
Fig. 25.—Female antennal ratios used by Reuter to separate *Orthotylus scotti* from *O. prasinus* showing lack of segregation. ●, specimens determined as *O. prasinus* by their K structures. ○, specimens labelled as *O. prasinus* in the British Museum collections. ■, specimens labelled as *O. scotti* in the British Museum collections. Ø, type of *O. scotti* Reuter. ⊘, specimens labelled as "Plum trees, Darenth, Scott," one of which must be regarded as the type of *Litosoma viridinervis* Douglas and Scott.

and also some other males and females determined by Reuter, which I have examined. The K structures of the bursa copulatrix of twenty females (two with antennal measurements very similar to the type) and the vesical appendages and claspers of several males (whose clasper position was the same as in those determined by Reuter) were dissected out and found in every case to be identical with those of *prasinus*. In my opinion *O. scotti* Reuter is synonymous with *O. prasinus* Fallén.

c. Key to the British species of the genus *Orthotylus* Fieber.

Note.—The average sizes and proportions appear in Table II, the length of hairs (of several species) in Table I; the ratio of the segments to the total length in fig. 45; diagrams of claspers in figs. 57–94; vesical appendages in figs. 95, 97–110, 115–118; and K structures in figs. 96, 136–152. The measurements of total length are those for the normal range.

1. Hemielytra with all or most erect hairs pale (figs. 52, 54) . . . . . 2.
Hemielytra with all erect hairs dark (black or deep brown) (figs. 53, 55, 56) . . . . 12.



FIGS. 26–33.—Terminal view of male genital segments. (26) *viridinervis.* (27) *marginalis.* (28) *ochrotrichus.* (29) *nassatus.* (30) *diaphanus.* (31) *prasinus.* (32) *rubidius.* (33) *virescens.*

2. Basal segment of the antennae sub-equal in length to head and with more than five long hairs (figs. 34, 40) . **viridinervis** (Kirschbaum, 1856)

A large green species, covered with pale hairs; antennae long, second segment with several exserted hairs; long hairs on underside of front femur; membrane pale, nervures green. ♂, 5·4–6·0 mm.; ♀, 5·0–6·0 mm.

Basal segment of antennae shorter than head and with less than five, or without, long hairs . . . . 3.

3. Basal segment of antennae without long hairs (fig. 37), apical segments shorter than basal . . . . **tenellus** (Fallén, 1829)

Small pale species, green when alive fading to yellow or fawn, covered with rather short pale hairs. ♂, 4·2–4·5 mm.; ♀, 4·1–4·5 mm.

Basal segment of antennae with four long hairs (three visible dorsally), apical joint longer than basal . . . . 4.

4. Head and pronotum entirely green or green with yellow . . . . . 5.
   Head and pronotum with dark markings, or entirely black, brown or yellow-red . . . . 11.

5. Large species, over 5·5 mm. in length (usually with yellow markings on the head, pronotum, scutellum and corium, and basal segment of antennae dark) . . . . 6.
   Smaller species, less than 5·5 mm. in length (usually entirely green and basal segment of antennae pale, *from the dorsal aspect*) . . . . 7.

6. Cell nervures bright yellow . . . . . . **flavinervis** (Kirschbaum, 1856)

   Very similar to *marginalis* in shape, but slightly smaller; colour varying from green to yellow, covered with pale hairs; first antennal segment brown or black in the male, yellow brown in the female, second segment yellowish, third and fourth dark brown; rostrum almost reaching apex of second coxa; membrane dusky, nervures yellow, contrasting with the green cuneus even when faded. ♂, 5·5–6·1 mm.; ♀, 5·5–6·0 mm.

   Cell nervures bright green (or if faded same colour as cuneus) **marginalis** Reuter, 1884

   Large species, male elongate, female oval, covered with pale hairs, mainly green, often with head, scutellum, margins of the pronotum, corium and anterior margin of the hind femur yellow; basal segment of antennae brownish, at least at the base, second segment yellow-brown, third and fourth brown; rostrum almost reaching apex of second coxa; membrane dusky. ♂, 6·0–6·5 mm.; ♀, 5·9–6·4 mm.

7. Underside of basal segment of antennae with a black line **nassatus** (Fabricius, 1797)

   A bright green species covered with pale hairs; rostrum almost reaching to the apex of second coxa; membrane pale grey, nervures bright green. ♂, 4·9–5·3 mm.; ♀, 4·7–5·1 mm.

   Underside of basal segment of antennae without a black line . . . 8.

8. Head, anterior part of the pronotum and base of scutellum more or less yellow-red, sides of corium bright yellow to yellow-red. Second segment of antennae with some medium hairs exserted (on Bay Willow (*Salix pentandra* L.)) . . . . **virens** Fallén, 1807 (Pale form—see below.)
   Without or with few yellow markings, these never yellow-red. Second joint with medium hairs not exserted . . . . 9.

9. Rostrum reaching just beyond apex of mesobasisternum (fig. 44), underside of front femur with a row of long hairs (fig. 38) **diaphanus** (Kirschbaum, 1856)

   A smallish species, pale green when alive fading to a very pale yellow; covered with erect pale and, especially on the cuneus, a few erect dark hairs, also adpressed dark hairs (fig. 54). Genitalia very small. ♂, 4·2–4·5 mm.; ♀, 4·5–4·75 mm.

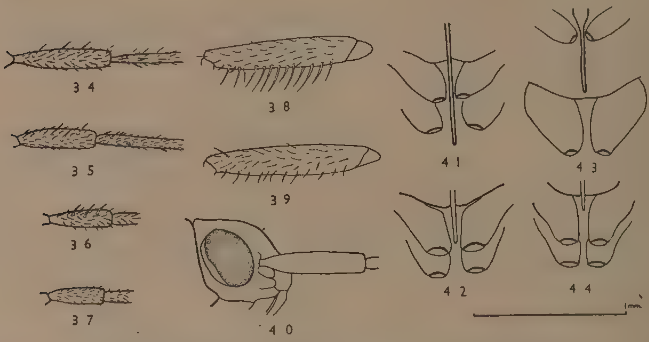
   Rostrum reaching well beyond apex of mesobasisternum, almost to apex of second coxa (fig. 42); underside of front femur without long hairs . . . . 10.

10. Male with right clasper flat, widely truncate (with two small processes) (fig. 78), left clasper with a row of spines visible along the dorsal margin (figs. 28, 90). Female with K structures with one sharply curved process (fig. 137). (Usually with vertex carinated and antennae less than 4·0 mm. in length) . . **ochrotrichus** (Fieber, 1864)

Medium sized bright green species, sometimes with yellow markings; covered with erect pale hairs; membrane pale, nervures green. ♂, 4·4–5·0 mm.; ♀, 4·7–5·1 mm.

Male with right clasper keeled and narrowly truncate (fig. 79), left clasper without or with only one or two spines visible along dorsal margin (figs. 31, 91). Female with K structures with three short blunt processes (fig. 138). (Usually with vertex ecarinate and antennae 4·0 mm. or more in length) . . . **prasinus** (Fallén, 1829)

Medium sized bright green species, very similar to the above and distinguished from it with certainty only by the genitalia; covered with erect pale hairs; membrane pale, nervures green. ♂, 4·9–5·3 mm.; ♀, 4·5–5·3 mm.



Figs. 34–37.—Dorsal view of basal and part of second antennal segments. (34) *viridinervis.* (35) *virens.* (36) *ochrotrichus.* (37) *tenellus.*

Figs. 38, 39.—Anterior view of front femur. (38) *diaphanus.* (39) *ochrotrichus.*

Fig. 40.—Lateral view of head and basal antennal segment of *viridinervis* to show relative lengths.

Figs. 41–44.—Ventral view of part of thorax to show length of rostrum. (41) *ericetorum.* (42) *ochrotrichus.* (43) *virescens.* (44) *diaphanus.*

11. Hemielytra yellow and/or green, without dark markings; second segment of antennae with medium length exserted hairs (fig. 35) **virens** (Fallén, 1807)

Medium sized, sub-elongate to oblong, covered with pale hairs; the coloration of the sexes differs.

Male: head black or brown with a pale median line, antennae brown or black; rostrum yellowish, reaching almost to apex of second coxa; pronotum entirely dark greenish-black, or yellow-green with anterior callosities brownish; scutellum black with two pale marks anteriorly, or yellow green, underside of thorax dark; legs yellowish, tarsi, especially the last segment, darker; hemielytra with clavus deep green, corium and cuneus greenish-yellow to yellow-red, or entirely yellow with base or corium and apex of cuneus yellow-red; membrane blackish with cell nervures yellow; abdomen black or yellow brown. 4·8–5·3 mm.

Female: head yellow-red, with, or sometimes without, darker markings, antennae pale brown; pronotum and scutellum yellow with yellow-red markings on anterior of pronotum and base of scutellum, sometimes darker markings especially at base of pronotum; underside of thorax yellow, hemielytra greenish, sides of corium and cuneus yellow to yellow-red ; abdomen yellow. 4·8–5·2 mm. Otherwise as male.

Dark, usually blackish, markings on the pronotum and hind margin of the clavus, scutellum with a median dark mark **bilineatus** (Fallén, 1807)

Sub-elongate, brownish to black species, with pale markings, covered with pale hairs ; underside greenish ; vertex carinated ; rostrum reaching just beyond mesobasisternum ; ground-colour variable from yellow brown to almost black. ♂, 4·8–5·5 mm. ; ♀, 4·8–5·1 mm.

12. Hemielytra with all hairs dark, none of adpressed type (fig. 53). (Rostrum reaching beyond apex of hind coxa (fig. 41) ; cell nervures bright yellow) . . . . **ericetorum** (Fallén, 1807)

Small bright green species covered with erect black hairs ; antennae yellow green, third and fourth segments brownish ; membrane grey brown. Wagner (1946) describes a new sub-species *carneae* from the Alps ; it may occur in mountain regions of Britain. The differences in the genitalia which his figures show may not, however, be true, as must of the figures for *ericetorum* proper (especially the right clasper and the dorsal vesical appendage) are not seen from the same angle as those of *carneae* and in my opinion do not show the structure correctly. ♂, 3·4–3·8 mm. ; ♀, 3·2–3·4 mm.

Hemielytra with erect dark and pale adpressed hairs (figs. 55, 56) . . 13.

13. Rostrum short, not reaching hind margin of mesobasisternum (fig. 43) (deep green, membrane dark) . **virescens** (Douglas & Scott, 1865)

A medium-sized to small species of a very intense green with yellow patches ; antennae yellow, except for basal joint, which is green ; membrane dark brown, nervures yellow-green near outer margin, but merging mesally (morphologically posteriorly) into a grey-brown colour like the membrane. ♂, 4·5–4·9 mm. ; ♀, 4·0–4·3 mm.

Rostrum reaching well beyond hind margin of mesobasisternum . . 14.

14. Species green . . . . 15.

Species reddish or brown . . . . 18.

15. Third joint of antennae short so that the second is greater in length than the third and fourth together ; rostrum reaching just beyond apex of second coxa . . . . **adenocarpi** (Perris, 1857)

Similar in size to the above but slightly broader and of a more yellowish-green. Antennae yellowish ; membrane pale grey-brown, nervures bright yellow green. ♂, 4·3–4·8 mm. ; ♀, 4·0–4·4 mm.

Not as above . . . . 16.

16. Cells unicolorous with the rest of membrane, grey-green, rostrum reaching almost to apex of third coxa . . **concolor** (Kirschbaum, 1856)

A smallish pale grey-green species, antennae and legs yellow brown, nervures pale green. ♂, 4·25 mm. ; ♀, 3·5–4·0 mm.

Cells of membrane green ; this may be pale . . . . 17.

17. Rostrum reaching to or beyond apex of third coxa ; small robust species under 3·5 mm. in length ; cells of membrane pale green **moncreaffi** (Douglas & Scott, 1875)

Small, but broad, green species. Membrane pale grey, cells and their nervures pale green. Formerly considered as a variety of *rubidius*, but raised to specific status by Wagner (1942), who showed it to be distinct in male genitalia, size and proportions, food plants and habitats. ♂, 2·7–3·2 mm. ; ♀, 2·9–3·3 mm.

Rostrum reaching only to apex of second coxa; larger species, over 3·5 mm.; cells of membrane bright green

flavosparsus (Sahlberg, 1874)

Bright green species; when living the patches of adpressed hairs appear macroscopically as silver dots. Antennae green, membrane pale grey. ♂, 3·7–4·1 mm.; ♀, 3·5–4·2 mm.

TABLE II.—*Average Measurements of the British* Orthotylus *spp.*

			Antennae.	Hemielytra.		Pronotum.	
Species.		Total length.	Length.	Length of cornified part.	Breadth.	Length.	Breadth at hind margin.
fuscescens	♂	4·80	3·00	3·00	0·75	0·55	1·30
	♀	4·30	2·83	2·85	0·80	0·55	1·35
bilineatus	♂	5·05	3·80	3·25	0·70	0·55	1·15
	♀	4·95	3·60	3·25	0·75	0·60	1·25
tenellus	♂	4·35	3·00	2·90	0·70	0·55	1·10
	♀	4·20	2·95	2·90	0·70	0·55	1·15
viridinervis	♂	5·65	4·55	3·85	0·85	0·65	1·30
	♀	5·60	4·45	3·85	0·90	0·65	1·35
marginalis	♂	6·20	4·05	4·25	0·95	0·80	1·50
	♀	6·15	4·00	4·10	1·05	0·80	1·60
flavinervis	♂	5·75	3·70	3·95	0·90	0·80	1·55
	♀	5·70	3·50	3·90	1·00	0·80	1·60
virens	♂	5·00	3·75	3·25	0·75	0·65	1·25
	♀	4·90	3·70	3·20	0·80	0·65	1·30
nassatus	♂	5·05	3·35	3·35	0·75	0·55	1·25
	♀	4·45	3·25	3·30	0·80	0·55	1·30
ochrotrichus	♂	4·75	3·76	3·25	0·75	0·55	1·15
	♀	4·85	3·85	3·40	0·80	0·55	1·25
prasinus	♂	5·05	4·00	3·40	0·75	0·50	1·25
	♀	4·90	4·15	3·30	0·80	0·55	1·25
ericetorum	♂	3·60	3·10	2·55	0·65	0·40	1·00
	♀	3·30	3·10	2·35	0·65	0·40	1·00
adenocarpi	♂	4·45	2·95	2·90	0·75	0·60	1·20
	♀	4·15	2·90	2·70	0·75	0·60	1·25
virescens	♂	4·70	3·50	3·20	0·80	0·60	1·15
	♀	4·15	3·20	2·85	0·80	0·60	1·25
concolor	♂*	4·25	3·10	2·70	0·65	0·50	1·10
	♀	3·80	2·80	2·50	0·65	0·50	1·05
flavosparsus	♂	3·85	3·05	2·70	0·60	0·45	1·00
	♀	3·90	3·35	2·80	0·75	0·45	1·25
rubidius	♂	2·70	2·25	1·70	0·50	0·40	0·90
	♀	3·00	2·55	1·85	0·60	0·40	1·00
moncreaffi	♂	3·00	2·40	1·95	0·60	0·40	0·95
	♀	3·25	3·00	2·25	0·65	0·45	1·10
diaphanus	♂	4·30	3·55	3·10	0·65	0·45	1·10
	♀	4·60	3·30	3·15	0·70	0·52	1·10

All measurements in mm. to the nearest 0·05 mm.

* Only one male *concolor* was examined; it was from the Edwards Collection, Norwich Castle Museum. In collections, at least, the female of the species is much commoner than the male.

18. Entirely olive brown, adpressed hairs long, rostrum reaching apex of second coxa . . . . **fuscescens** (Kirschbaum, 1856)

Unicolorous species, erect hairs dark brown (fig. 56); vertex carinated; membrane dusky, nervures olive brown. ♂, 4·5–5·1 mm.; ♀, 4·0–4·6 mm.

Reddish green to red, adpressed hairs shorter, rostrum reaching to apex of second coxa . . . . **rubidius** (Puton, 1877)

A small reddish species, antennae and legs light red-brown; membrane (including cells) pale grey-brown, nervures red. ♂, 2·7–3·2 mm.; ♀, 2·9–3·3 mm.

d. Structure of the Genus.

Historical Review.

The genus *Orthotylus* Fieber, 1858, *sensu lato,* occurs according to Carvalho (1952) in Europe, North and South America, Africa and Hawaii. There have been many attempts to subdivide *Orthotylus.* Reuter (1875) listed four sub-genera: *Orthotylus,* Fieber *sensu stricto* (Kirkaldy 1906 fixed the type as *nassatus* Fabricus, 1787), *Melanotrichus* Reuter, 1875, *Allocotus* (Fieber) Puton, 1874 and *Litocoris* Fieber, 1860.

Litocoris was a new name for *Tichorhinus* Fieber, 1858 (type *Lygaeus ericetorum* Fallén, 1807), *now Tichorhinus* Brandt, 1849 (Mammalia); *Tichorinus* Kirkaldy, 1906, and *Tichorrhinus* Oshanin, 1912, also were mispellings of this name. The character of this sub-genus was reputed to be " mucro prostethii convexiusculus," but this is not satisfactory.

Allocotus (type *A. rubidius* (Fieber) Puton, 1874), was shown by Puton (1878) to be preoccupied; he proposed the name *Halocapsus* in its place. Wagner (1942) redefined the sub-genus (containing *rubidius* (+ form *salsolae*) *minutus*, *schoberiae*, *moncreaffi* and *palustris*), and showed it to have definite characters in the male genitalia. He mentions that *flavosparsus* and *diaphanus* are intermediate in position.

Melanotrichus Reuter, for which Kirkaldy (1906) designated *flavosparsus* Sahlberg as type, was raised by Knight (1927) to generic status, its characters being " dorsum bearing two types of pubescence, simple hairs intermixed with recumbent, scale-like pubescence; left genital clasper represented by a simple hook, not bifurcate into nearly equal parts, as in typical *Orthotylus.*" However, this statement about " typical *Orthotylus* " only applies to *marginalis*, *flavinervis* and *virens* (possibly also to *nassatus*) in the pale-haired British species (figs. 85–87, 89). American authors have continued to classify species into the separate genera, *Orthotylus* and *Melanotrichus.* Recently Carvalho and Leston (1952) have separated the British species; *Melanotrichus* (containing *flavosparsus*, *virescens*, *concolor*, *adenocarpi*, *rubidius*, *moncreaffi* and *ericetorum*) is distinguished by the possession of mixed pubescence.

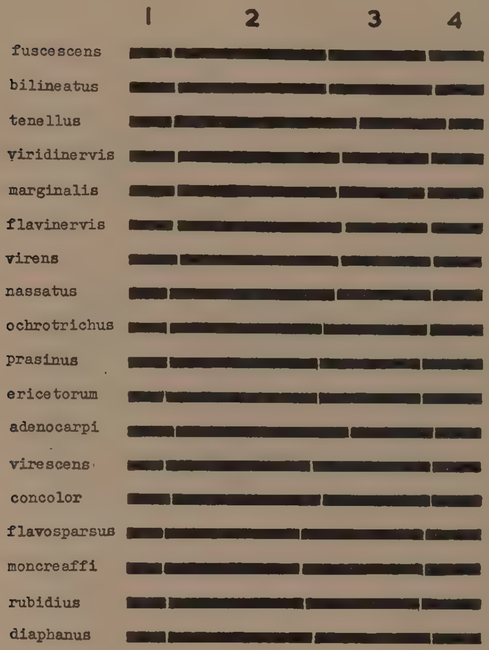
Comparative Characters.

The major characters that have been or may be used in the division of the genus must now be considered:

(1) *Antennae.*

i. Hairs. In all species the arrangement is similar (fig. 36), except in *tenellus* (fig. 37), *viridinervis* (fig. 34) and *virens* (fig. 35).

ii. Relative lengths of the segments.—These are shown in diagrammatic form (fig. 45) and it will be seen that in general they support the grouping suggested later. There is a trend towards the equalisation of the lengths of the second and third segments, the only exceptions being *tenellus* with the short apical and *adenocarpi* and *boreellus* with the short third segment.



45

Fig. 45.—The length of the antennal segments as a proportion of total antennal length.

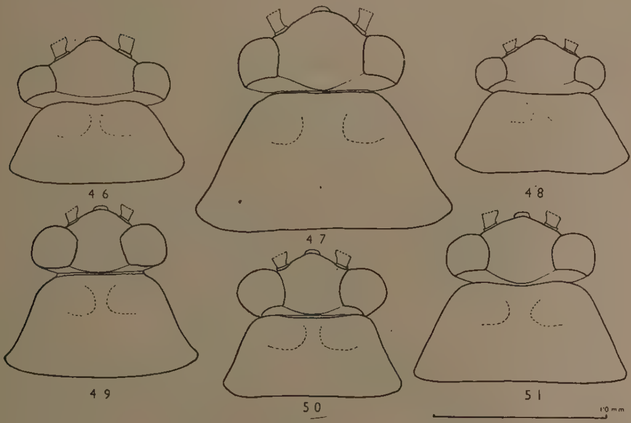
(2) *Rostrum length.*—The rostrum is very short in *virescens* (fig. 43) (as in *Pachylops* Fieber, but not thickened apically); of medium length, reaching beyond the mesobasisternum, but not beyond the apex of the second coxa, in most species (figs. 42 and 44), long, reaching almost to or beyond the apex of the third, in *concolor*, *ericetorum* (fig. 41), *rubidius* and *moncreaffi*.

(3) *Vertex width/eye width ratio.*—This is a secondary sexual character, the males always having larger eyes and smaller vertices than the female (Table III and figs. 46–51). In *bilineatus* and *diaphanus* the ratio is particularly low, approaching that found in *Cyrtorhinus* Fieber, *Mecomma* Fieber and related genera.

TABLE III.—*Vertex width/Eye width Ratios*

Sex.	*fuscescens.*	*bilineatus.*	*tenellus.*	*viridinervis.*	*marginalis.*	*flavinervis.*	*virens.*	*nassatus.*	*ochrotrichus.*	*prasinus.*	*ericetorum.*	*adenocarpi.*	*virescens.*	*concolor.*	*flavosparsus.*	*rubidius.*	*moncreaffi.*	*diaphanus.*
Male . . .	1·9	1·0	1·3	1·8	1·7	1·7	1·7	2·0	2·0	1·9	2·7	2·1	1·5	1·9*	1·9	2·1	2·3	1·1
Female . . .	2·2	1·4	2·1	1·9	1·9	1·9	1·9	2·4	2·2	2·0	2·8	2·4	2·1	2·1	2·1	2·4	2·7	1·6

* See footnote to Table II.



FIGS. 46–51.—Head and pronotum of male. (46) *flavosparsus.* (47) *marginalis.* (48) *ericetorum.* (49) *bilineatus.* (50) *diaphanus.* (51) *nassatus.*

(4) *Pubescence.*—This has been widely used by various authors and it must be stressed that there are more types than have been recognised. These are now :

i. Erect pale hairs only as in *bilineatus*, *tenellus*, *viridinervis*, *marginalis* (fig. 52), *flavinervis*, *virens*, *nassatus*, *ochrotrichus*, *prasinus*, *boreellus*, *dorsalis*.

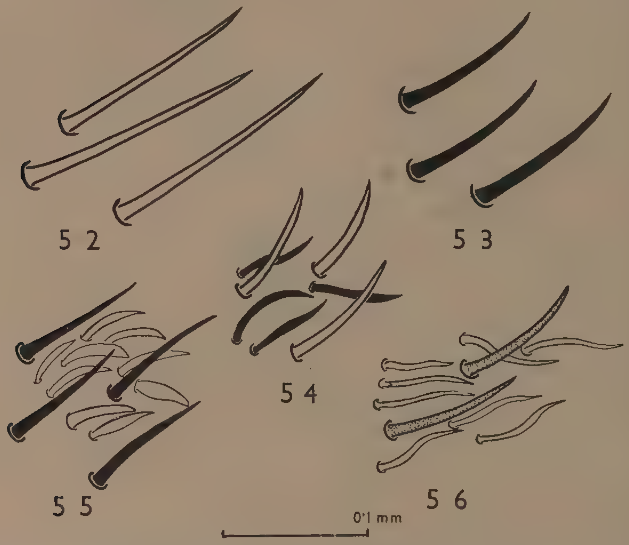
ii. Erect pale hairs (with an occasional dark one, especially on the cuneus) mixed with adpressed dark ones, as in *diaphanus* (fig. 54).

iii. Erect black hairs only, as in *ericetorum* (fig. 53).

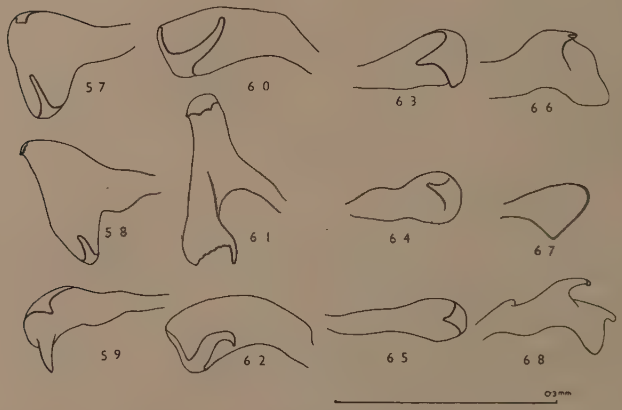
iv. Erect black hairs with short adpressed curled pale ones that are slightly longer, as in *adenocarpi*, or shorter as in *fieberi*, *flavosparsus* (fig. 55), *minutus*, *rubidius*, *moncreaffi*, *iolani*, *concolor* and *virescens*.

v. Erect dark brown hairs with adpressed pale ones, as in *fuscescens* (fig. 56).

(5) *Pronotum.*—This varies considerably from the more elongate almost campanulate shape in *bilineatus* (fig. 49), through the typical straight-sided form, as in *nassatus* (fig. 51), to the very broad form in *ericetorum* (fig. 48) and *moncreaffi*.



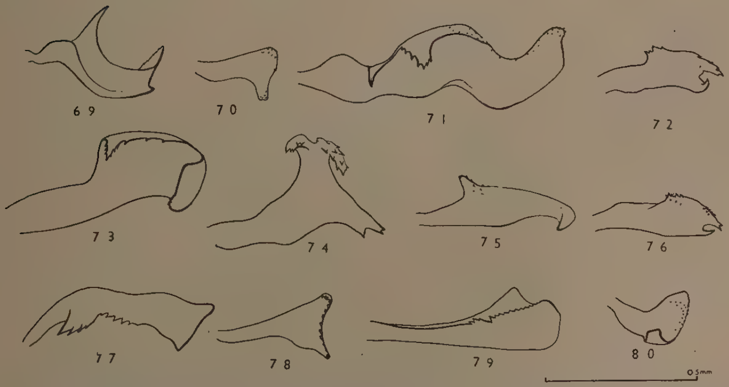
Figs. 52–56.—Hemielytral pubescence. (52) *marginalis*. (53) *ericetorum*. (54) *diaphanus*. (55) *flavosparsus*. (56) *fuscescens*.



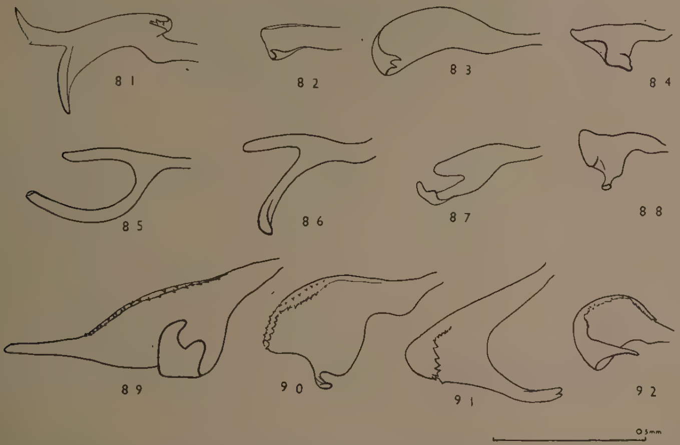
Figs. 57–62.—Left clasper (inner, morphologically median, view).
Figs. 63–68.—Right clasper (inner, morphologically median, view). (57, 63) *moncreaffi*. (58, 64) *rubidius*. (59, 65) *diaphanus*. (60, 66) *virescens*. (61, 67) *flavosparsus*. (62, 68) *concolor*.

(6) *Genitalia.*

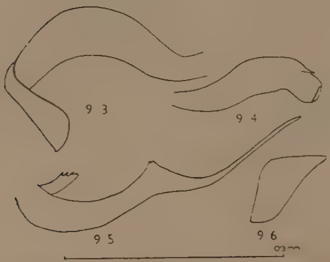
i. Claspers: the right clasper is more simple, much smaller and spoon-shaped in *moncreaffi*, *rubidius*, *diaphanus*, *flavosparsus*, *fieberi* and *iolani* (figs. 63–65, 67, 113, 114); small, but with a longer process, as in *virescens* and *concolor* (figs. 66 and 68); it is larger and spinose in the other species examined (figs. 69–80), except in *bilineatus* (fig. 94).



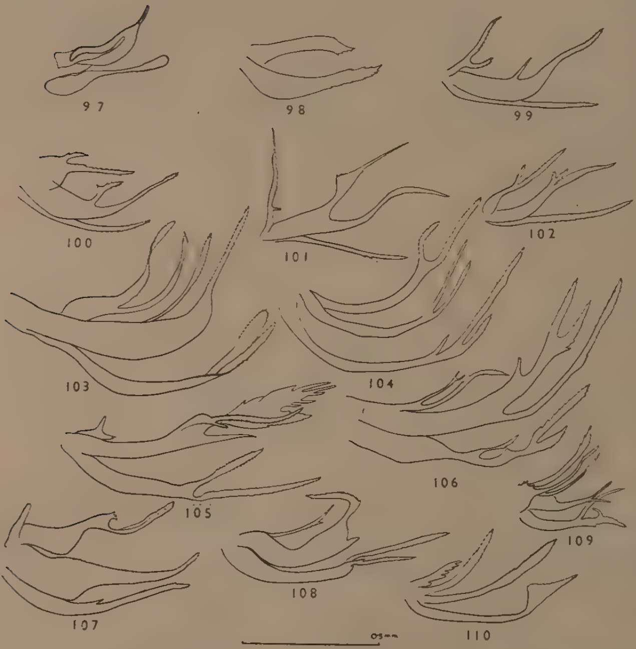
Figs. 69–80.—Right clasper (inner, morphologically median, view). (69) *fuscescens.* (70) *tenellus.* (71) *viridinervis.* (72) *boreellus.* (73) *marginalis.* (74) *flavinervis.* (75) *virens.* (76) *adenocarpi.* (77) *nassatus.* (78) *ochrotrichus.* (79) *prasinus.* (80) *ericetorum.*



Figs. 81–92.—Left clasper (inner, morphologically median, view). (81) *fuscescens.* (82) *tenellus.* (83) *viridinervis.* (84) *boreellus.* (85) *marginalis.* (86) *flavinervis.* (87) *virens.* (88) *adenocarpi.* (89) *nassatus.* (90) *ochrotrichus.* (91) *prasinus.* (92) *ericetorum.*


93
94
95
96
0·3 mm

FIGS. 93–96.—Genitalia of *bilineatus*. (93) left clasper (inner view). (94) right clasper (inner view). (95) vesical appendages. (96) K structures.


97
98
99
100
101
102
103
104
105
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107
108
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110
0·5 mm

FIGS. 97–110.—Vesical appendages of the aedaegus. (97) *fuscescens*. (98) *concolor*. (99) *virescens*. (100) *adenocarpi*. (101) *viridinervis*. (102) *boreellus*. (103) *marginalis*. (104) *nassatus*. (105) *ericetorum*. (106) *prasinus*. (107) *flavinervis*. (108) *ochrotrichus*. (109) *tenellus*. (110) *virens*.

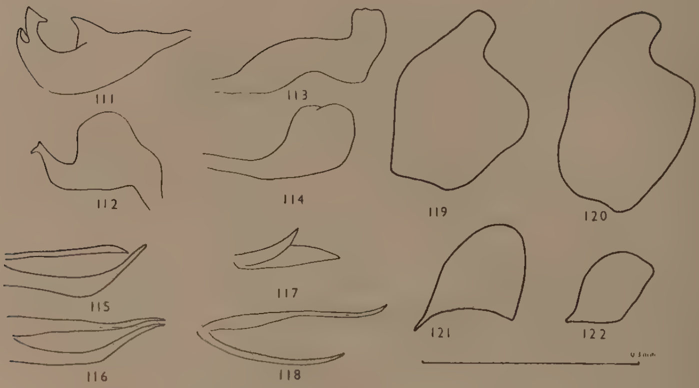
The left clasper is diverse in its structure and divides the genus into several distinct groups, which are described in the next section.

- *ii. Theca* and *vesical appendages*; these fall into four groups:
  - *a.* Strongly sclerotised, theca with lateral curved outgrowths, vesical appendages smooth, as in *fuscescens* (fig. 97).
  - *b.* Strongly sclerotised, theca simple boat-shaped, vesical appendages unbranched and simple, as in *bilineatus* (fig. 95).
  - *c.* Strongly sclerotised, theca simple boat-shaped (fig. 24), vesical appendages with numerous teeth and much branched, as in most species (figs. 98–110).
  - *d.* More weakly sclerotised, theca more tubular, vesical appendages much smaller, smooth and little branched (very difficult to extract from theca), as in *diaphanus*, *fieberi* (fig. 116), *flavosparsus* (fig. 118), *minutus*, *rubidius*, *moncreaffi* (fig. 117) and *iolani* (fig. 115).
- *iii. Second valvulae of ovipositor:* These fall into two groups:
  - *a.* Apex symmetrically pointed, as in *fuscescens* (fig. 130) (and *Pachylops bicolor*).
  - *b.* Apex asymmetrically pointed, as in the other species examined (figs. 123–129, 131–135).
- *iv. K structures of the bursa copulatrix:* Broadly these fall in three groups:
  - *a.* Large anterior margin with one or more processes, as in most species (figs. 119, 120, 136–146).
  - *b.* Smaller, anterior margin smooth, as in *diaphanus*, *flavosparsus*, *fieberi*, *minutus*, *rubidius* and *moncreaffi*, *iolani* (figs. 121, 122, 147–150), with a slight projection, *virescens* (fig. 151) or with a rounded projection, *concolor* (fig. 152).
  - *c.* Small, triangular in shape, with apex sharply pointed, as in *bilineatus* (fig. 96).

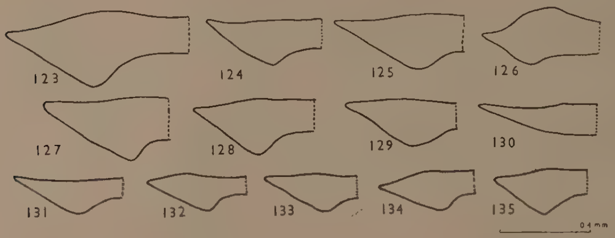
Note.—So far as I am aware the K structures have not previously been used to separate closely allied species. Therefore it should be stressed that their shape (and that of the vesical appendages) is very constant. The K structures were dissected from 25 *prasinus*, 15 *ochrotrichus*, and from at least 2 (usually about 4) specimens of every other British species; in *fuscescens* only one was examined. The vesical appendages were examined in 5 or more specimens of the following species, *bilineatus*, *marginalis*, *prasinus* and *ericetorum*.

Discussion.

It will be seen from the above that there is no sharp division of *Orthotylus sensu lato* into *Orthotylus sensu stricto* and *Melanotrichus*, though the differences between the respective types are clear cut. The character used in marking this division has been pubescence, but in this case it does not seem reliable. For example, *adenocarpi* closely resembles *boreellus* in genitalia (especially the male) and in the short third antennal segment, so that it cannot be put in the same sub-genus as *flavosparsus* (with which pubescence is its only similarity), and *boreellus* in another.



FIGS. 111, 112.—Left clasper (inner view). (111) *fieberi.* (112) *iolani.*
FIGS. 113, 114.—Right clasper (inner view). (113) *fieberi.* (114) *iolani.*
FIGS. 115–118.—Vesical appendages. (115) *iolani.* (116) *fieberi.* (117) *moncreaffi.* (118) *flavosparsus.*
FIGS. 119–122.—K structures of bursa copulatrix. (119) *boreellus.* (120) *dorsalis.* (121) *iolani.* (122) *fieberi.*



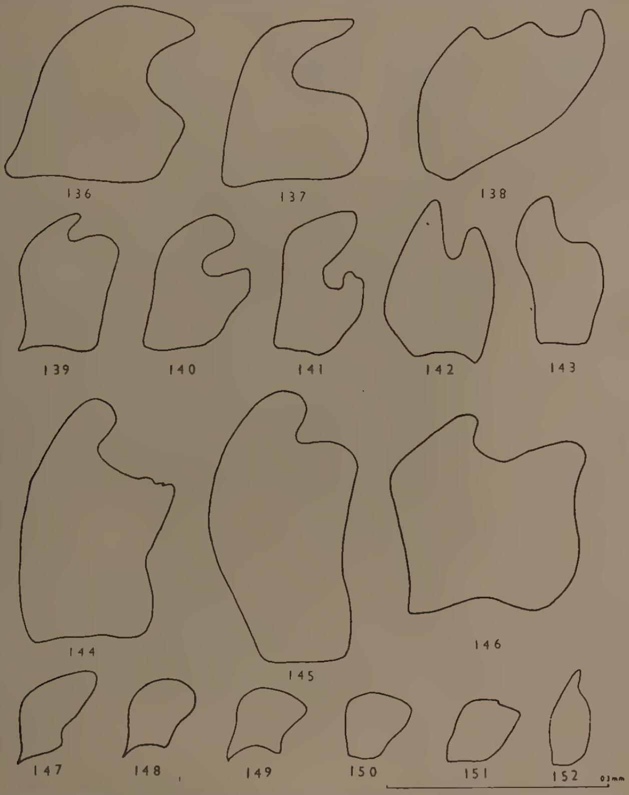
FIGS. 123–135.—Apex of second valvulae of ovipositor. (123) *flavinervis.* (124) *diaphanus.* (125) *viridinervis.* (126) *ericetorum.* (127) *virens.* (128) *prasinus.* (129) *ochrotrichus.* (130) *fuscescens.* (131) *tenellus.* (132) *moncreaffi.* (133) *flavosparsus.* (134) *adenocarpi.* (135) *nassatus.*

Orthotylus sensu lato cannot be divided into two separate genera ; if it is to be divided into genera there will have to be at least four, based on a combination of characters including genitalia. The use of such internal characters is clearly undesirable, and in spite of divergences in head and thorax proportions, genitalia, rostrum length and pubescence as great as that between some Orthotyline genera, there is a definite overall similarity between the species. It seems probable that *Orthotylus* is close to the ancestral Orthotyline stock, for a genus or group of genera of this tribe frequently appears to be allied to a certain species or species group within *Orthotylus* itself.

Therefore it is proposed to subdivide the genus into four sub-genera as follows :

(1) **Pinocapsus** subgen. n.

Pubescence of brown erect and adpressed white hairs (fig. 56) ; theca with lateral outgrowths ; vesical appendages smooth, but strongly sclerotised (fig. 97) ; ovipositor with second valvulae symmetrically pointed (fig. 130) ; K structures with two straight processes on anterior margin (fig. 142), living on conifers. Type *fuscescens* Kirschbaum.



FIGS. 136–152.—Dorsal view of left K structures of bursa copulatrix. (136) *nassatus.* (137) *ochrotrichus.* (138) *prasinus.* (139) *virens.* (140) *adenocarpi.* (141) *ericetorium.* (142) *fuscescens.* (143) *tenellus.* (144) *flavinervis.* (145) *marginalis.* (146) *viridinervis.* (147) *flavosparsus.* (148) *moncreaffi.* (149) *rubidius.* (150) *diaphanus.* (151) *virescens.* (152) *concolor.*

(2) **Neomecomma** subgen. n.

Eyes large, in male equal to and in female about two thirds vertex width ; pronotum with very narrow depressed collar visible anteriorly and sides sinuate (fig. 49) ; male genitalia with two simple curved claspers (figs. 93, 94) and vesical appendages unbranched and simple (fig. 95); apex of second valvulae of ovipositor asymmetrically pointed, K structure small and triangular (fig. 96). Type *bilineatus* Fallén.

Judging from Knight's (1923) figures of the claspers, *O. candidatus* Van Duzee is certainly very close to *bilineatus* and also belongs to this sub-genus. The genital characters, besides the large eyes, point to this sub-genus being close to *Mecomma* Fieber (including *Antiphilus* Distant, and Carvalho and Leston (1952) have suggested *Cyrtorhinus* Fieber), *Paraproba* Distant and related genera. Both *bilineatus* and *candidatus* occur on Aspens, *Populus tremula* and *P. tremuloides* respectively.

(3) *Orthotylus* Fieber, 1858, *sensu stricto.*

Male genitalia strongly sclerotised, theca boat shaped, vesical appendages much branched and toothed, right clasper usually spinose; K structures with a process or indentation on the anterior margin. Type (fixed by Kirkaldy, 1906) *nassatus* (Fabricus). Species included in the sub-genus are grouped as follows:

a. marginalis group: vertex/eye ratio comparatively low; pronotum with very narrow depressed "collar" visible, margins very slightly sinuate (fig. 47); covered with pale erect hairs only (fig. 52); male with left clasper deeply bifurcate (figs. 85–87). Occurring on various members of the Amentaceae. Also including *flavinervis* and *virens* from Europe, *dorsalis*, *modestus* and many other species from North America.

b. nassatus group: vertex/eye ratio somewhat higher, no trace of pronotal collar visible dorsally, sides of pronotum straight (fig. 51); covered with pale erect hairs; male with left clasper spinose, with long curved process from ventral margin (figs. 89–91). Mainly arboreal species. Also including *ochrotrichus* and *prasinus*.

c. adenocarpi group: based mainly on the essential similarity of the male genitalia, the left clasper with a curved ventral process (as in *nassatus* group), but lacking spines (figs. 66, 68, 84, 88), while the vesical appendages show a definite pattern which is best seen from figs. 99, 100, 102; *concolor* (fig. 98) differs, showing that the details of structure are not completely reliable (see also in *marginalis* and *flavinervis*).

The claspers, vesical appendages and K structures point to certain species being isolated; this is supported by other structures:

d. viridinervis: long antennae (so that basal segment is longer than head), with many long hairs (at least this character is shared by *Canariocoris* Lindberg).

e. tenellus: antennae with apical segment shorter than basal, which lacks long hairs, pubescence in general short, vertex/eye ratio small especially in the male.

f. ericetorum: vertex/eye ratio high, pronotum broad (fig. 48); covered with erect black hairs; rostrum long, reaching to or beyond apex of third coxa; apex of second valvulae of ovipositor unique.

(4) *Melanotrichus* Reuter, 1875.

Vesical appendages more weakly sclerotised, small, unbranched and toothless (figs. 115–118), theca more tubular; right clasper simple spoon-shaped, K structures small and rounded. Type (fixed by Kirkaldy, 1906), *flavosparsus* Sahlberg; also includes *fieberi*, *minutus*, *rubidius*, *moncreaffi*, *iolani*, *diaphanus*. A definite species group within the sub-genus is formed by Puton's sub-genus *Halocapsus*; this is dealt with in detail by Wagner (1942), and he lists, besides the type, *rubidius*, the following: *schoberiae* Reuter, *minutus* Jak., *moncreaffi* D. and S., *palustris* (Reut.). A completely isolated position is occupied by *diaphanus*, differing as it does from other *Melanotrichus* spp. in the short rostrum, reaching only just beyond posterior margin of mesobasisternum, vertex/eye ratio low, only just more than one in the male; covered with pale, and a few dark, erect and dark adpressed hairs.

Note.—Only species that were examined are listed under each sub-genus. Besides material from Britain, specimens of *fuscescens*, *bilineatus*, *tenellus*, *viridinervis*, *marginalis*, *flavinervis*, *virens*, *nassatus*, *prasinus*, *ericetorum*, *adenocarpi*, *virescens*, *flavosparsus* and *moncreaffi* from the continent of Europe and of *flavosparsus* from U.S.A. were examined; also the following non-British species: *dorsalis* (Provancher) U.S.A.; *modestus* Van Duzee, U.S.A.; *boreellus* (Zetterstedt), Scandinavia; *fieberi* (Frey-Gessn.), S. Russia; *minutus* Jakovl, S.E. Europe and Turkestan; *iolani* Kirkaldy, Hawaii.

e. Check list of the British species

China (1943) listed eighteen species from Britain; this list must now be revised, for, as shown above, *O. scotti* is synonymous with *O. prasinus* and *O. moncreaffi* was added as a valid species by Carvalho and Leston (1952).

Orthotylus Fieber, 1858.

Type *nassatus* Fabricus, 1787.

Synonyms or included genera:

Tichorhinus Fieber, 1858, *non* Brandt, 1849, type *ericetorum* Fallén, 1807.
Litocoris Fieber, 1860, type *ericetorum* Fallén, 1807.
Litosoma Douglas and Scott, 1865, type *marginalis* Reuter, 1884.
Allocotus (Fieber) Puton, 1874, *non* Mayr, 1864, type *rubidius* (Fieber) Puton, 1874.
Halocapsus Puton, 1878, type *rubidius* (Fieber) Puton, 1874.
Melanotrichus Reuter, 1875, type *flavosparsus* Sahlberg, 1842.
Diommatus Uhler, 1887, type *dorsalis* Provancher, 1872.
Tichorinus Kirkaldy, 1906, error pro *Tichorhinus* Fieber, 1858.
Tichorrhinus Oshanin, 1912, error pro *Tichorhinus* Fieber, 1858.

Sub-genus **Pinocapsus subgen. n.**

fuscescens (Kirschbaum, 1855).

Sub-genus **Neomecomma subgen. n.**

bilineatus (Fallén, 1807).
    kirschbaumi (Flor, 1860).

Sub-genus *Orthotylus* Fieber, 1858, *sensu stricto*.

tenellus (Fallén, 1829).
    angustus (Herrich-Schaeffer, 1835).
viridinervis (Kirschbaum, 1856).[1]
marginalis Reuter, 1884.
    nassatus (Fallén, 1829, followed by Fieber, 1861, Douglas and Scott, 1865, *non* Fabricus, 1787).
flavinervis (Kirschbaum, 1856).
    ? *iterocephalus* Hahn, 1831.

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[1] Carvalho and Leston (1952) have pointed out in a footnote to their paper that, although 1855 is on the title-page of *Jb. nassau. Ver. Naturk.* **10**, it was in fact published the following year.

virens (Fallén, 1807).
nassatus (Fabricus, 1787).
    striicornis (Kirschbaum, 1856, followed by Flor, 1860, Fieber, 1861, Douglas and Scott, 1865).
ochrotrichus (Fieber, 1864).
    propinquus Reuter, 1878.
prasinus (Fallén, 1829).
    scotti Reuter, 1877.
    viridinervis (Douglas and Scott, 1865, *non* Kirschbaum, 1856).
ericetorum (Fallén, 1807).
    limbatus (Mulsant et Rey, 1857).
adenocarpi (Perris, 1857).
    douglasi Saunders, 1875.
virescens (Douglas and Scott, 1865).
    chloropterus (Kirschbaum, 1856, *non* Herrich-Schaeffer, 1850).
    concolor (Douglas and Scott, 1865, *non* Kirschbaum, 1856).
concolor (Kirschbaum, 1856).

Sub-genus *Melanotrichus* Reuter, 1875.
flavosparsus (C. Sahlberg, 1842).
    viridipennis (Sahlberg, 1850).
    prasinus (Douglas and Scott, 1865, *non* Fallén, 1829).
rubidius ((Fieber) Puton, 1874).
moncreaffi (Douglas and Scott, 1874).
    curvipennis Reuter, 1875.
diaphanus (Kirschbaum, 1856).

3. SUMMARY.

An account is given of the general morphology of *Orthotylus* Fieber, 1858; especially that of the female genitalia and the sclerotised structures within the head.

O. scotti Reuter is shown to be synonymous with *O. prasinus* Fallén.

The British species are keyed, with brief descriptions.

A comparative account, with figures and measurements, is given of the antennae, pronotum and pubescence; the genitalia (claspers and vesical appendages in the male, second valvulae and K structures of the bursa copulatrix in the female) are also figured.

The structure of the genus is discussed and it is divided into four subgenera, two of which are new.

4. ACKNOWLEDGMENTS.

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SEXUAL DIMORPHISM IN THE SECOND INSTAR OF SOME DIASPIDIDAE (HOMOPTERA : COCCOIDEA).

By K. L. BORATYŃSKI, Ph.D., D.I.C., F.R.E.S.

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With 6 Text-figures.

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INTRODUCTION.

OBSERVATIONS on the species studied in the present work and other available information show that the postembryonic development of Diaspididae comprises 3 instars in the female and 5 in the male. These are respectively : 1st larva (crawler), 2nd larva and adult female, and 1st larva (crawler), 2nd larva, prepupa, pupa and adult male. Börner (1910) incorrectly reported 6 instars in the male of *Aulacaspis rosae* (Bouché) (see below). The subject of the present paper is a study of the morphology and sexual differences of the 2nd (larval) instar.

The "macroscopic" sexual differences in this instar, such as the different shape and colour of the body, absence or presence of pigmented eye-spots and rudiments of pupal appendages in the two sexes, have been discussed by several authors (Felt, 1901; Newstead, 1901; Quayle, 1911; Nel, 1933; Carmin and Sheinkin, 1934; Jones, 1936; Mathis, 1947). These characters, however, are of little real value, since they are the result of growth within the 2nd instar or of the development of the next instar and are therefore apparent only some time after the first moult, or shortly before the second one. Comparatively little is known about differences in the microscopic structures. The published observations on the morphology of this instar usually refer only to the female series (Thiem and Gerneck, 1934; Bonnemaison, 1936; Ferris, 1938–1942; Moutia, 1944; Lupo, 1944), and generally confirmed Berlese's earlier (1896) observation that, except for the considerable reduction in the number of gland-ducts, and absence of the vulva and perivulvar derm pores, the 2nd instar female is similar to the adult female. Some information on the 2nd instar male, available for 10 species in all, was provided by Berlese[1] (1896), Börner[2] (1910), Stickney[3] (1934), Lombardi[4] (1938), and Geier[5] (1949). No obvious sexual dimorphism was found in the development of the pygidium and pygidial marginal structures in the eight species studied by Berlese, Stickney and Lombardi. Some degree of sexual differentiation, although different in different species, was apparent in the development of the glandular system. Thus in *Aspidiotus hederae* the female has slightly fewer pygidial macroducts than the male, but in *Parlatoria zizyphus* the number of both the macroducts and the prepygidial plates of the female is considerably less (Berlese, *l.c.*). In *P. blanchardii*, however, the male and the female in this instar are very similar in all respects (Stickney, *l.c.*). In *Targionia vitis* the female differs from the male in having somewhat fewer and smaller pygidial macroducts, and no "pori marginali" i.e., a series of short macroducts on the lateral margins of the intermediate segments of the body characteristic of the male, (Lombardi, *l.c.*).

Thus, on the basis of the above information, and taking the development of the pygidium as the measure of sexual differentiation, the very close similarity of the 2nd instar female and male was generally assumed (Balachowsky, 1939: 220). Ferris (1942, S.IV 446: 6), however, while admitting the similarity of the two sexes at this stage in the species which have been carefully studied (particularly *P. blanchardii*), suggested, on the basis of some of his material, "that in at least some species it [the male] may be quite different in its pygidial structures." This suggestion proved true of *Epidiaspis leperii*, in which the female shows the usual conditions of well-developed pygidium, and the male differs in having no sclerotized pygidium and no pygidial marginal structures; in addition, the number of ducts in the male is considerably greater and include two types, "pointes filières" (gland tubercles) and "pores à cupule" (cup-like pores), which do not occur in this instar of the female (Geier, *l.c.*).

---

[1] *Aspidiotus hederae* (Vallot), *Parlatoria zizyphus* (Lucas), *Chrysomphalus ficus* Ashm., *Aonidiella aurantii* (Mask.), *Lepidosaphes beckii* (Newm.), *L. ulmi* (L.).

[2] *Aulacaspis rosae* (Bouché).

[3] *Parlatoria blanchardii* (Targ.).

[4] *Targionia vitis* Sign.

[5] *Epidiaspis leperii* Sign.

Börner (1910) described in some detail the developmental stages of both male and female in *Aulacaspis rosae* (Bouché). He recognized 3 instars in the female series and in the male 6, namely 3 larval and 2 pupal instars and the imago. Börner considered that the 3 larval instars of the male corresponded directly with the 3 instars of the female. In the present study, however, a series of specimens of *A. rosae* at various stages of the moulting process of all instars was carefully examined and showed only 5 instars in the male. The accuracy of Börner's descriptions and drawings permits the following identification of the instars which he described : his 2nd instar of the male and the 2nd instar of the female both represent the 2nd instar of the female, the former being a young individual and the latter a fully grown one of the same instar ; his 3rd instar of the male is the true 2nd instar of the male, and comes directly from the 1st larval instar after the first moult of the insect[6]. Thus, the similarity of the early instars of the two sexes is not so close as supposed by Börner, and the actual conditions are very similar to those described by Geier in *E. leperii*.

Material.

The following species were studied :

Tribe Aspidiotini.	Tribe Diaspidini.
Diaspidiotus bavaricus (Lindinger).	*Lepidosaphes ulmi* (Linnaeus).
Quadraspidiotus ostreaeformis (Curtis).	*Carulaspis* sp.
Quadraspidiotus zonatus (Frauenfeld).	*Chionaspis salicis* (Linnaeus).
	Aulacaspis rosae (Bouché).

There is also some reference to sexual dimorphism, but without detailed description of the larvae, in *Lepidosaphes tuberculata* Malenotti, found by Dr. W. F. Jepson on a " lily " growing under glass at Titness Farm, Sunninghill, Berks. Some information about the 2nd instars of *L. ulmi* and *A. rosae* was given by Berlese and Börner respectively (*op. cit.*).

The material was collected during the seasons 1949/50 and 1950/51 at Imperial College Field Station, Silwood Park, Sunninghill, Berks., where the observations on the life-histories of these species were originally carried out. The descriptions of the larvae were based on at least ten specimens of each species and each sex from a single host species harbouring both sexes ; the drawings were made with a camera lucida, and represent as accurately as possible the specimens actually drawn. The observations on the scales produced by each sex in this instar were made with regard to the differences in external appearance and relative texture and thickness (volume), but without accurate measurements.

The life cycle of each species, as observed at Silwood Park in 1949/51, is given in an abbreviated form, the following symbols being used : E, –eggs ; L1, and L2, –1st and 2nd larval instars respectively ; Pp, and P, –prepupa, and pupa ; M, –adult male ; F, –adult female ; W–, –overwintering period. The Roman figure, with the fractional number, –the month, and part of the month in which the particular instar appears in the field. Thus, the formula for the male *D. bavaricus* is given as follows :

---

[6] This can be clearly seen on preparations of the individuals immediately before the first moult showing the 2nd instar still enclosed within the skin of the 1st instar (" pharate 2nd instar."—Hinton, 1946, 1948).

$$\text{E, }\tfrac{1}{2}\text{VI–}\tfrac{1}{2}\text{VII ; L1, VII ; L2, }\tfrac{3}{4}\text{VII–W–}\tfrac{1}{2}\text{IV ; Pp, IV ; P, }\tfrac{3}{4}\text{IV–}\tfrac{3}{4}\text{V ; M, V.}$$

which should be read : the eggs are to be found from the middle of June till the middle of July ; the 1st instar in July ; the 2nd instar from the end of July, throughout the winter, till the middle of April ; prepupae in April ; pupae from the end of April till the third week in May ; the adult males in May.

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NOTES ON THE SPECIES STUDIED AND ON THEIR LIFE CYCLES.

(1) *Diaspidiotus bavaricus* (Lindinger) (=*Aspidiotus bavaricus* Lindinger, 1912).

Prior to 1912 this species was not separated from *A. ostreaeformis* Curtis, e.g., the specimens on *Calluna* sp. from Kent, England, recorded by Newstead (1901, **I** : 102).

At Silwood Park it is abundant on *Calluna vulgaris* Salisb. ; also collected by the author at Bagshot, Oxshott and Wimbledon Common (Surrey) from the same host, and at Golden Cap (Dorset) from *Erica cinerea* L. The specimens on *Calluna vulgaris* from Silwood Park were used for studies.

Life cycle : Univoltine.

$$\text{E, }\tfrac{1}{2}\text{VI–}\tfrac{1}{2}\text{VII ; L1, VII ; }\begin{array}{l}\text{L2, }\tfrac{3}{4}\text{VII–W–}\tfrac{1}{2}\text{IV ; Pp, IV ; P, }\tfrac{3}{4}\text{IV–}\tfrac{3}{4}\text{V ; M, V . ♂}\\ \text{L2, }\tfrac{3}{4}\text{VII–W–}\tfrac{1}{2}\text{V ; F, V–VI . . . . ♀}\end{array}$$

Parasites : From ♀ scales collected in June, 7 ♀ and 2 ♂ *Aphycus* sp. emerged in the laboratory in July.

(2) *Quadraspidiotus ostreaeformis* (Curtis) (*Aspidiotus ostreaeformis* Curtis, 1843).

At Silwood Park the species occurs in crowded but localized colonies on some branches of *Betula alba* L. and this material was used for studies.

Life cycle : Univoltine.

$$\text{E, VI–VII; L1, VII–}\tfrac{1}{4}\text{VIII; }\begin{array}{l}\text{L2, VIII–W–IV; Pp, and P, IV–V; M, }\tfrac{3}{4}\text{V–}\tfrac{1}{4}\text{VI ♂}\\ \text{L2, VIII–W–V; F, V–VII . . . . ♀}\end{array}$$

Parasites : From ♀ scales collected in March–April, 1 ♂ and 1 ♀ *Prospaltella* sp., and 1 ♀ *Perissopterus* sp. emerged in the laboratory in May–June.

Some individuals of this species were found scattered on the bark of twigs and branches of *Carpinus betulus* L. which was growing close to the infested birch, with the trunks of both trees touching each other and with the crowns overlapping. Examination in July and August showed that some of the scales contained still living larvae of the 1st and 2nd instars. About 100 scales examined during the period October to May contained only dead bodies of the immature stages, but a young female, or an old female with eggs or egg-shells, was never encountered. This fact would suggest that the full development was never completed on this host, and the immature individuals probably represented accidental immigrants from the birch. *A. ostreaeformis* has been recorded on *Carpinus betulus* in Europe (Lindinger, 1912; Szulczewski, 1926; Kawecki, 1935).

(3) *Quadraspidiotus zonatus* (Frauenfeld) (=*Aspidiotus zonatus* Frauenfeld, 1868).

At Silwood Park abundant on *Quercus robur* L., and in some numbers on *Quercus cerris* L. The female scales occur on the bark of the twigs and branches, the male " puparia " on the underside of leaves. On three occasions in September single scales containing normal young females were found on the underside of the leaves of *Q. robur*; the shape of these scales was typical of the normal female scale, but their colour was much brighter, similar to that of the male puparium. The specimens from *Quercus robur* were used for studies.

Life cycle : Univoltine.

E, ½V–¼VI; L1, VI–½VII; L2, ¼VII–¼VIII; Pp, and P, VIII–IX; M, IX . ♂
L2, ½VII–½VIII; F, VIII–W–V . . . . . ♀

Parasites : From the ♀ scales collected in June 2 ♂ and 1 ♀ *Pteroptrix ? dimidiata* Westw., 1 ♀ *Prospaltella* sp. and 1 ♀ *Aphycus ? aonidiae* Merc. emerged in the laboratory in June. From the ♂ scales collected in August 1 ♂ *Pteroptrix ? dimidiata* Westw. and 1 ♀ *Aphelinus ? aonidiae* Merc. emerged in the laboratory in September.

(4) *Lepidosaphes ulmi* (Linnaeus, 1758) (=*Mytilaspis pomorum* Bouché, 1851).

At Silwood Park this species occurs in numbers on *Calluna vulgaris* Salisb., *Crataegus oxyacantha L.*, and on apple trees in the orchards; single specimens were taken from *Achillea millefolium* L. and *Fagus sylvatica* L. At Boxhill, Surrey, some specimens were found on *Mentha* sp., *Polygala vulgaris* L. and *Origanum vulgare* L.; also on *Erica Tetralix* L. and *Potentilla* sp. at Golden Cap, Dorset. Both sexes together were found on *Calluna vulgaris* and this material was used for studies.

Life cycle : Univoltine.

E, ½VIII–W–½V; L1, V–½VI; L2, VI–VII; Pp, and P, ½VII–½VIII; M, VIII ♂
L2, VI–¼VIII; F, ½VII–VIII . . . . . ♀

(5) *Carulaspis* sp.

At Silwood Park the species was found on *Juniperus sinensis* L., both in the open and in a conservatory; the specimens from the host plant growing in the open were used for studies. Both host plants were later cut down and removed, *Life cycle :* Univoltine (both in the open and in the conservatory, but the dates refer to the specimens in the open).

E, $\frac{1}{2}$V–VI : L1, VI ; L2, $\frac{1}{2}$VI–VII ; Pp, and P, VII–VIII ; M, VIII ♂
L2, $\frac{1}{2}$VI–VIII ; F, $\frac{1}{2}$VIII–W–V . . . . . ♀

The nomenclature of this species will have to remain uncertain until some revisional work is done ; such work is beyond the scope of the present study, but some results of the preliminary observations should be mentioned. The following four (at least) names are involved : *Coccus visci* Schrank described from *Viscum album* ; *Aspidiotus juniperi* Bouché, *Diaspis carueli* Targ. and *D. minima* Targ. from conifers of the type *Cupressus* and *Juniperus.* Lindinger (1911, 1912), Leonardi (1920), Ghesquière (1933), Lupo (1938), considered these names as synonymous and representing one species, i.e., *C. visci* Schr. This opinion of European workers was accepted, though somewhat doubtfully by Ferris (1937, S.I. 12). Examination of a series of adult females, including the specimens in the British Museum (N.H.), reveals, however, that the specimens involved can be separated into three groups on the basis of two characters, namely (1) the presence or absence of a large marginal tubular duct between the median lobes of the pygidium, and (2) the presence or absence of a single submarginal macroduct posterior to the 5th abdominal segment. The taxonomic importance of these characters cannot be established until a detailed study of individual variation on larger samples of specimens from various hosts and localities is made ; but the examination of 30 adult females from *Juniperus sinensis* at Silwood Park showed that in these specimens the two characters are constant and not subject to individual variation. These females belong to group (1), consisting of specimens *with* a large marginal duct between the median lobes, and *without* the submarginal macroduct posterior to the 5th abdominal segment. Identical conditions were found in the specimens on the slide labelled *Diaspis minima* Targ. (B.M., Newstead's Coll., *ex* coll. K. L. Kafka, Wien, 1897 ; host plant not recorded). Similar are the specimens labelled *D. carueli* or *D. visci* from Juniper (*ex* coll. C. V. Riley and R. N.), *Cupressus lawsoniana* (England), *Juniperus tamariscifolia* (Belgium), *Wellingtonia* (France) (B.M. Collection), and the specimens recently received from Mr. V. Fowler, Entomologist at the R.H.S. Gardens, Wisley, from *Chamaecyparis nutkatensis* var. *glauca* Beiss.

Group (2) comprising specimens *without* the large marginal duct between the median lobes of the pygidium and *without* a submarginal duct posterior to the 5th abdominal segment, is represented in the British Museum by specimens on several slides labelled *D. carueli* Targ. from *Thuja occidentalis* and *Juniperus virginiana* (Kew Gardens, England) (cf. Newstead, 1901, **I** : 162–165), *Thuja* and *Cupressus* (various localities in Egypt—coll. W. J. Hall), and from *Cupressus* (Santiago, Chile). Apparently similar specimens were used by Leonardi (1920) and Lupo (1938) for their discussion of *C. visci* (Schrank). In the opinion of Borkhsenius (1950) the specimens without the duct between the median lobes (key character) represent *C. minima* (Targ.).

Group (3) consists of specimens *with* a large macroduct between the median lobes and *with* a single submarginal duct posterior to the 5th abdominal segment ; these conditions are shown by all the 11 specimens on a slide labelled *Diaspis visci* (Schrank) from *Viscum album* (B.M., Newstead's coll. *ex* coll. K. L. Kafka, Wieu, 1897), and are similar to those described by Ferris (1937, S.I.12) except in the actual position of the single submarginal macroduct posterior to the 5th segment.

(6) *Chionaspis salicis* (Linnaeus, 1758).

At Silwood Park this species occurs on *Alnus glutinosa* Gaertn., *Salix* sp., and *Tilia* sp. ; the specimens from a well-established colony on *Tilia* were taken for studies.

Life cycle : Univoltine.

E, VIII–W–V ; L1, VI ; L2, $\frac{3}{4}$VI–VII ; Pp, and P, $\frac{3}{4}$VII–VIII ; M, VIII . ♂
L2, $\frac{3}{4}$VI–VIII ; F, VIII–$\frac{1}{2}$IX . . . . ♀

(7) *Aulacaspis rosae* (Bouché, 1833).

At Silwood Park a small colony of this species was found on a rose-bush growing in the middle of an overgrown rose-bed. When, however, in the course of time, the bed was thinned and the infested bush exposed, the colony completely disappeared during the following winter.

Life cycle : Univoltine.

E, VIII ; L1, VIII–IX ; L2, IX–W–VI ; Pp. and P, VI–VII ; M, $\frac{3}{4}$VII–VIII ♂
L2, IX–W–VII ; F, VII–VIII . . . . ♀

In Great Britain the life cycle of this species may apparently differ from the above (season 1949/50 at Silwood Park). Newstead (1901, **I** : 171–172) stated that in the wild colonies in Cheshire and Gloucestershire, " before the winter sets in the male larvae effect their first moult, and a small portion of puparium is formed ; but the female larvae do not moult until the following spring and may be found throughout the winter, either permanently fixed, or active even during severe frosts." He observed the males swarming on 19th May, 1896, but recorded also that Mr. Green obtained males in August, 1895, which in Newstead's opinion was " probably a case of retarded development." Newstead also remarked that the species " loves sheltered hedgerows." At Guernsey (C.I.) the pupae of males, adult males, young adult females, females already ovipositing and a number of young crawlers were observed by the author to occur simultaneously on *Rubus fruticosus* at the beginning of July, 1949. In the Paris area in France hibernation takes place at the adult female stage, the eggs are deposited in the spring, and the 1st instar larvae appear in the middle of May or beginning of June (Balachowsky and Mesnil, 1936, **II** : 1560). It would appear that in England, apparently the northern flank of the distribution, the climate is too severe (? cool summer) for the establishment of the regular life cycle of the insect and its survival, except in sheltered positions.

III. MORPHOLOGY OF THE 2ND INSTAR OF THE SPECIES STUDIED.

General observations.

All the species studied share certain features which will be discussed first, in order to avoid unnecessary repetition later.

Shape and size of the body.—Immediately after the first moult the 2nd instar male and female show no appreciable difference in shape and size, both sexes being oval, or broadly oval, and small. During the following growing period the female gradually assumes a form approaching that of the adult female of the particular species. The male, on the other hand, assumes a shape similar in all species, becoming elongated, more or less parallel-sided, with both ends broadly rounded; shortly before the second moult the rudiments of prepupal appendages are visible through the transparent larval skin. The relative size, as expressed by the length of the body of the fully grown male and female insects in this instar, varies in different species. In *L. ulmi* the fully grown 2nd instar female is about 1·5 the length of the fully grown male 2nd instar, but in *D. bavaricus* or *Q. zonatus* the length of the fully grown 2nd instar of the two sexes differs little if at all.

Dorsal derm.—Before the second moult the dorsal derm of the female becomes heavily sclerotized, and, after the moult, incorporated into the waxy scale which is finally completed by the adult female. The derm of the male insect remains membranous (except the pygidium, if present), and, after the moult, is pushed back and finally out from under the scale (cf. Ferris, 1942, S.IV, 446 : 6). There is no change in the volume and appearance of the male "puparium" after the second moult of the insect, and microscopical examination showed that the prepupa and pupa have no ducts at all; thus, in the male the scale produced by the 2nd instar is the final one.

Segmentation of the body.—As indicated by the intersegmental sutures this is more distinct in the male and always more apparent on the prepygidial part of the abdomen; the head, pro-, meso-, and often metathorax are more or less fused. In the male of Diaspidini the submarginal ventral areas of the 1st and 2nd, and the 3rd and 4th abdominal segments often are fused.

Body setae.—The segmentation is also indicated by segmentally arranged body setae, which form four well-defined longitudinal series: marginal, submarginal ventral, subventral and subdorsal. The most conspicuous is the *marginal series*, which is well developed in all species, forming a partly double marginal row composed of 2 setae on each segment except on the 1st and 2nd abdominal segments (which always appear to carry only one), and on the marginal area of the head (which bears several scattered, slightly larger setae). Posteriorly the setae of this series become the large marginal setae marking the fused segments of the pygidium. In Aspidiotini the last segment of the pygidium carries only one seta situated dorsally at the base of the outer margin of the median lobes; in Diaspidini there are three setae at the base of each median lobe, two being dorsal and one ventral. The *submarginal ventral*, *subventral* and *subdorsal* series each form a more or less complete single longitudinal row composed of one seta on each segment, the setae being very inconspicuous, often shorter than the diameter of the minute basal disc. The development of these series varies in different species and in the two sexes within a species; in some (*L. ulmi*) both sexes have all the rows present and complete, but in others (*C. salicis*, *A. rosae*) the rows are more or less reduced or even absent, the female showing a greater degree of reduction. Some irregularities frequently occur, e.g., a particular segment may carry two setae, or none at all, instead of the usual one.

Glandular system.—As in the adult females, the 2nd instar larvae of species belonging to the tribes Aspidiotini and Diaspidini differ markedly in the structure of the ducts and in the general pattern of the glandular system, and within each tribe there are different types of sexual dimorphism.

In Aspidiotini the " one-barred " macroducts, usually very *long*, occur on the pygidium where they form characteristic rows and groups ; these groups are either almost identical in both sexes (*D. bavaricus*), or composed of fewer ducts in the female (*Q. zonatus*). On the prepygidial segments there are no macroducts in the female except for the sporadic and irregular occurrence of a single short macroduct ; in the male, however, there is a series of conspicuous, *short* but comparatively wide macroducts (*marginal ducts*—" pori marginali," Lombardi, *l.c.*) occurring regularly and in constant numbers on the margins of the mesothorax, metathorax and 1st abdominal segment. This feature is diagnostic for the separation of the two sexes. The *microducts*, with simple openings on the surface of the body, are present in both sexes and are arranged in three longitudinal series, *marginal*, *subdorsal* and *subventral*, the series being irregular and the number of ducts in each variable ; the marginal series extends from mesothorax to 6th abdominal segment, and the other two are limited to the prepygidial segments. A few scattered microducts occur on the head and on the sternal area of the thorax.

In Diaspidini the conditions are more varied. The sexual differences are shown usually in considerable reduction in the numbers of ducts in the female, and, in some species, in structural modification of some ducts in the male. The " two-barred " macroducts are arranged in longitudinal series, of which the following are recognized here to facilitate the descriptions : (1) *Large macroducts* in a single row on the margin of the pygidium composed of four or five ducts on each side, beginning with the space between the median and second lobes. In the female 2nd instar this series is always present and normally developed. In the male of some species (*L. ulmi*) it is also well and normally developed, but in others (*Carulaspis* sp., *A. rosae*) the glands of this series are modified into cup-like pores (" pores à cupule " Geier, *l.c.*) and, as in *C. salicis*, the posterior section of the series is missing. The structure of these modified glands is not properly understood. They appear to have the external opening in the form of a shallow, sclerotized, cup-like depression with a short and narrow membraneous duct which opens in the centre of the bottom of the depression ; the inner end of the duct is considerably enlarged, lens-like in section, with an obscure " two-barred " structure. The most anterior cup-like glands of this series occurring on the fused submarginal ventral area of the 3rd and 4th abdominal segments are often arranged in a characteristic and conspicuous group of 2 or 3 ducts, each duct with a distinct sclerotized kidney-shaped external opening (figs. 5A, 6A). (2) The *smaller macroducts* are arranged in three longitudinal series : (A) marginal, (B) subventral and (C) subdorsal. The ducts of the *marginal series* occupy a wide marginal area on the mesothorax, metathorax and on the 6 or 7 anterior abdominal segments. On the metathorax and on the 1st abdominal segment the ducts are most numerous and they are arranged there in transverse clusters or bands reaching far on to the venter ; posteriorly, in the area where the margin is occupied by the large pygidial ducts, this series is divided into two submarginal rows, (*a*) submarginal ventral and (*b*) submarginal dorsal. The other two series, the *subventral* and *subdorsal*, are confined to the abdominal segments, where they form either short single or double rows composed of 1 or 2 ducts on each segment, or, as in *L. ulmi*, short bands made up of 3–4 ducts in a transverse row on each segment. All the series of these smaller macroducts are more or less complete in the male. In the female they are always reduced, being at most incomplete (*L. ulmi*) and often absent altogether, except for a few ducts in the submarginal ventral and subventral series (*Carulaspis* sp., *C. salicis*, *A. rosae*). A few macroducts occur scattered in the cephalic area and on the ventral part of the thorax. The size of the macroducts of an individual varies considerably, decreasing anteriorly and towards the mid-line of the body, while the ducts of the ventral surface are smaller than those of the dorsum. The smallest macroducts are often not much larger than the microducts. The *microducts* are associated with *gland spines* (slender, membraneous) and *gland-tubercles* (stout, enlarged and slightly sclerotized at base) (cf. Ferris, 1942, S.IV, 446 : 12). Typical gland-spines occur on the margins of the posterior abdominal segments, especially on the pygidium; gland-tubercles, on the other hand, occur in subventral groups on the mesothorax, metathorax and anterior abdominal segments. These conditions were found in the 2nd instar larvae of both sexes of *L. ulmi* (and *L. tuberculata*). In the other three species studied the conditions are different, showing some differences in the development of these structures in the species, and considerable differences in the two sexes within a species. Thus, in the female of *A. rosae* and *C. salicis* the subventral groups on the thorax, and the marginal series on the abdomen (including pygidium), are composed of similar gland-spines which together form a continuous longitudinal series extending from the mesothorax to the 8th abdominal segment. In the female of *Carulaspis* sp. the gland-spines are limited to the marginal row on the pygidium, there being no spines or tubercles on the anterior abdominal segments and thorax. In the male of all three species the gland tubercles are well developed and arranged in the usual subventral groups on the mesothorax, metathorax and the fused area of the 1st and 2nd abdominal segments. The gland spines on the margins of the posterior abdominal segments (including the pygidium) of the males are reduced to small "raised glands" (Stickney, 1938) in *C. salicis* and *A. rosae*, and are completely absent in *Carulaspis* sp. Corresponding with the conditions in the adult female, a pair of gland spines between the median lobes is present in *L. ulmi* and *Carulaspis* sp., and absent in *C. salicis* and *A. rosae*.

The *pygidium* is always present and well developed in the female 2nd instar, being similar to that of the adult female (except for the reduced number of ducts and for the absence of the vulva and perivulvar derm pores). In the male the conditions vary. The species studied can be arranged in a sequence from those in which the male has the pygidium well developed and identical with that of the female in this instar, to those species in which the pygidium and the corresponding structures are completely absent in the male. The three species of Aspidiotini occupy the beginning of this sequence, all having the pygidium well developed in both sexes; the Diaspidini show a wide range of variation, from *L. ulmi* with a well-developed pygidium in both sexes, to *A. rosae*, the male of which has no pygidium; *Carulaspis* sp. and *C. salicis* are intermediate.

Eyes.—The eyes in the form of simple convex sclerotizations, are always present in the male, though they are sometimes very inconspicuous. In the female the conditions vary; the eyes may be present in the form of simple sclerotizations as in the male (*C. salicis*, *A. rosae*, *Q. ostreaeformis*), or developed as small eye-tubercles (?) (*L. ulmi*), or they are so inconspicuous as to escape observation and are possibly absent (*D. bavaricus*, *Q. zonatus*, *Carulaspis* sp.).

The following structural details, though different in different species, are identical in both male and female 2nd instar of each species :

Antennae : Always in the form of a small tubercle with one or more apical, subapical, or basal setae. *Legs :* Not observed, probably absent. *Spiracles :* Two thoracic pairs, with bar, the bar of the anterior spiracle longer. In Diaspidini the anterior spiracles have one or more disc pores anterior to the spiracular opening. *Labium :* Globular or conical. The internal loop of the mouth-stylets (within the crumena) is long and doubly bent in the individuals immediately after the moult (fig. 5) ; later it appears to become progressively shorter (fig. 3B).

(1) *Diaspidiotus bavaricus* (Lindinger). Specimens from *Calluna vulgaris.*

The 2nd instar larvae of the two sexes are very similar. During the overwintering period (July–February) the greyish-black or blackish-brown *scales* of both sexes are identical in external appearance, texture and thickness (volume). From about the second half of February the male " puparium " gradually becomes elongated, with a whitish rim appearing along the sides and posterior end ; the female scale remains oval. The *body* is at first similar in both sexes, oval, tapering posteriorly and yellow. In the spring the male becomes elongated, and the female gradually enlarged anteriorly, assuming a broadly oval or circular shape. Fully grown 2nd instar larvae of both the male and female are of about the same length.

Microscopic structures (fig. 1).—*Segmentation* of body obscure, the intersegmental sutures of prepygidial abdominal segments more distinct in male. *Pygidium* large, well sclerotized in both sexes, composed of the 4th and following segments ; in male, a short transverse suture partially separates the 4th segment from the rest. *Body setae* in the usual series : on pygidium without subdorsal series but with one or two additional setae between subventral and submarginal ventral rows. *Antennae* small, rugose tubercles with one slightly curved lateral seta. *Spiracles* subequidistant from mid-line and margin, with bar gradually enlarged and reticulate medially. *Eyes* small, simple convex sclerotizations in the male ; not observed in female. *Labium* conical, with round base. *Anal opening* posterior to the centre of pygidium ; small, its diameter about the length of median lobes and at a distance of about 3 times this diameter from the posterior apex. *Marginal structures* of pygidium identical in both sexes, except lobes in male slightly smaller. *Lobes :* only median pair developed, projecting posteriorly, longer than wide, parallel, each with margin notched on both sides ; the second pair marked by small unsclerotized points. *Marginal setae* well developed, slightly longer than the lobes. *Plates :* one pair between median lobes, slender, simple or shallowly bifid ; two between the median lobes and the setae marking the 7th segment, plate nearer median lobe simple and slender, the other wider and secondarily subdivided ; two or three plates between setae marking the 7th and 6th segments, with slight tendency for male to have 3 plates in this position (average of 20 specimens : 2·5 for female, 2·9 for male) ; if three plates present, the two more median ones slender and simple, if only two the median plate deeply bifid. No microducts associated with these plates. Beyond the setae marking the 6th segment two small membraneous prominences each with opening of a microduct at base. *Macroducts* "one-barred": the *long ducts* on dorsal surface of pygidium arranged in groups and rows composed of similar numbers of ducts in both sexes ; between the median lobes a single duct with its inner end reaching the anal opening ; between the median lobe and the setae of the 7th segment a marginal cluster of 3 ducts; between the setae of 7th and 6th segments one marginal duct and opposite it a short longitudinal row of 3–4 ducts, average 3·3 for both sexes; between the setae of 6th and 5th segments two submarginal ducts arranged in line parallel to the margin, and, opposite the more lateral duct, a row of 2–3 ducts in female

FIG. I. D. bavaricus (Ldgr.)

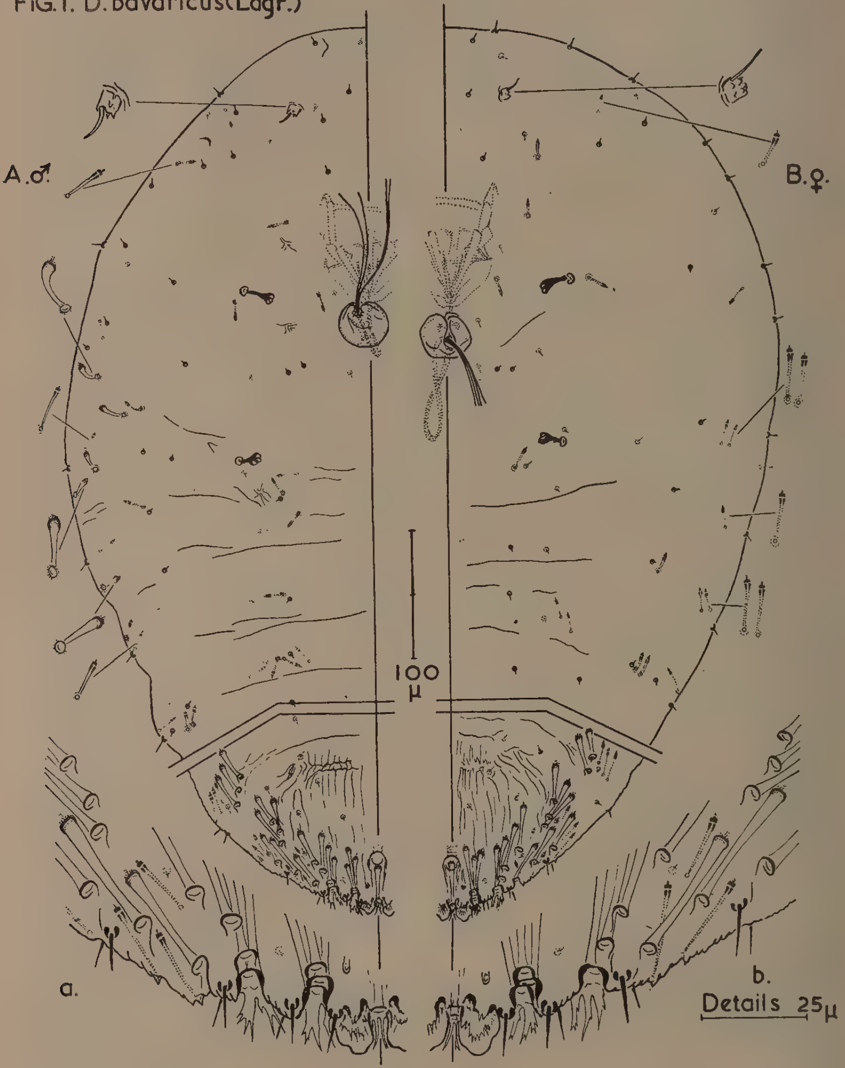

Fig. 1.—*Diaspidiotus bavaricus* (Lindinger). A, male; B, female; anterior part of the body in ventral aspect, the pygidium in dorsal aspect. *a*, *b*, details of pygidium of male and female, respectively, in dorsal aspect. The structures of the respective opposite sides in dotted lines.

and 3–4 ducts in male (average 2·95 and 3·3 respectively); beyond the setae marking 5th segment a single submarginal duct, sometimes missing in the female (average 0·75). On the 4th segment a subdorsal group of 2–3 ducts (average 2·8 for male and 2·3 for female). *Marginal* series of *short macroducts* characteristic of male, composed of 2 ducts on mesothorax, 2 on metathorax and 1 on the 1st abdominal segment. Among 20 females examined two individuals were found with one short macroduct on one side of the body, on the 1st abdominal segment and the metathorax respectively. *Microducts*, extremely small, often escaping observation. The marginal series extends from mesothorax to 6th abdominal segment; ducts on pygidium occupying marginal and submarginal ventral position, those on prepygidial segments scattered over a wide marginal area, the number of ducts varying from 2 to 4 on segments 3–6, decreasing irregularly to a single one in mesothorax. Subventral and subdorsal series irregular, the number of ducts varying individually; in female often reduced, represented by one or two ducts on only one prepygidial segment. A few microducts scattered on anterior part of the body and on the sternal area of the thorax.

(2) *Quadraspidiotus ostreaeformis* (Curtis). Specimens from *Betula alba.*

During the overwintering period (August–February) the *scales* produced by the two sexes in the 2nd instar are very similar in external appearance, texture and volume; the male " puparium " becomes elongate in early spring. The *body* is at first similar in both sexes, small, oval, yellowish; in spring the male becomes elongate, and the female broadly oval with pointed posterior apex. Lengths of fully grown male and female 2nd instar larvae are about the same.

Microscopic structures.[7]—*Segmentation* of body less distinct than in the previous species. *Pygidium* large, broad, with acute apex, composed of 4th and following segments; well sclerotized, except for partly membraneous 4th segment. *Body setae:* marginal series well developed; subdorsal and subventral series irregular, the pygidial section of the former missing. *Antennae* conical, slender, with pointed apex and one curved seta arising at the base anteriorly. *Spiracles* subequidistant from margin and mid-line, with narrow bar slightly enlarged and reticulate at the median end. *Eyes* simple, convex sclerotizations present in both sexes, in male more conspicuous. *Labium* conical with oval base. *Anal opening* small, its diameter about the length of median lobes, at a distance of about 2·5 times this diameter from posterior apex. *Marginal structures* of the pygidium very similar in both sexes. *Lobes,* two pairs well developed, in the male slightly smaller; median lobes close to each other, with outer margin distinctly notched; second lobes smaller, with sloping outer margin. Third lobes indicated by small sclerotized points. *Marginal setae* slender, rather long, longer than lobes. *Plates:* one pair between median lobes, slender and simple; two plates between median and second lobes, and two between second lobe and setae of the 6th segment—in both these series the more median plate is simple and slender, and the more lateral one wide and more or less subdivided. No microducts associated with these plates. Beyond the setae of the 6th segment one or two small membraneous prominences, each with the opening of a microduct at its base. *Macroducts* " one-barred ": *long macroducts* on dorsal surface of pygidium arranged in groups and rows, composed of slightly fewer ducts in female; between median lobes a single duct with its inner end reaching the anal opening; between median and second lobes a marginal cluster of 2–3 ducts in female and 2–4 in male (average 2·05 and 3·05 respectively); between second lobe and setae of 6th segment one marginal duct, and opposite it an oblique row composed of 2–4 ducts in female, and 3–5 in male (average 3·05 and 4·0 respectively); between setae of 6th and 5th segments two submarginal ducts arranged in a line parallel to the margin—in male both ducts always present, in female the more lateral one often missing (average

[7] The anatomical details, including the distribution and arrangement of the ducts of this species, show great similarity with the preceding species; its illustration is therefore omitted, but reference to fig. 1 should help in locating the structures here discussed.

0·5) ; opposite the more lateral duct (or in corresponding position if it is missing) an oblique row of 2–4 ducts in female and 3–5 in male (average 3·0 and 3·5 respectively) ; beyond the setae of 5th segment often a single duct in male (average 0·85), and none in female. On 4th segment usually one subdorsal duct in both sexes (range 0–2, average 1·0). The number of ducts in any group varies within the given ranges not only in various individuals

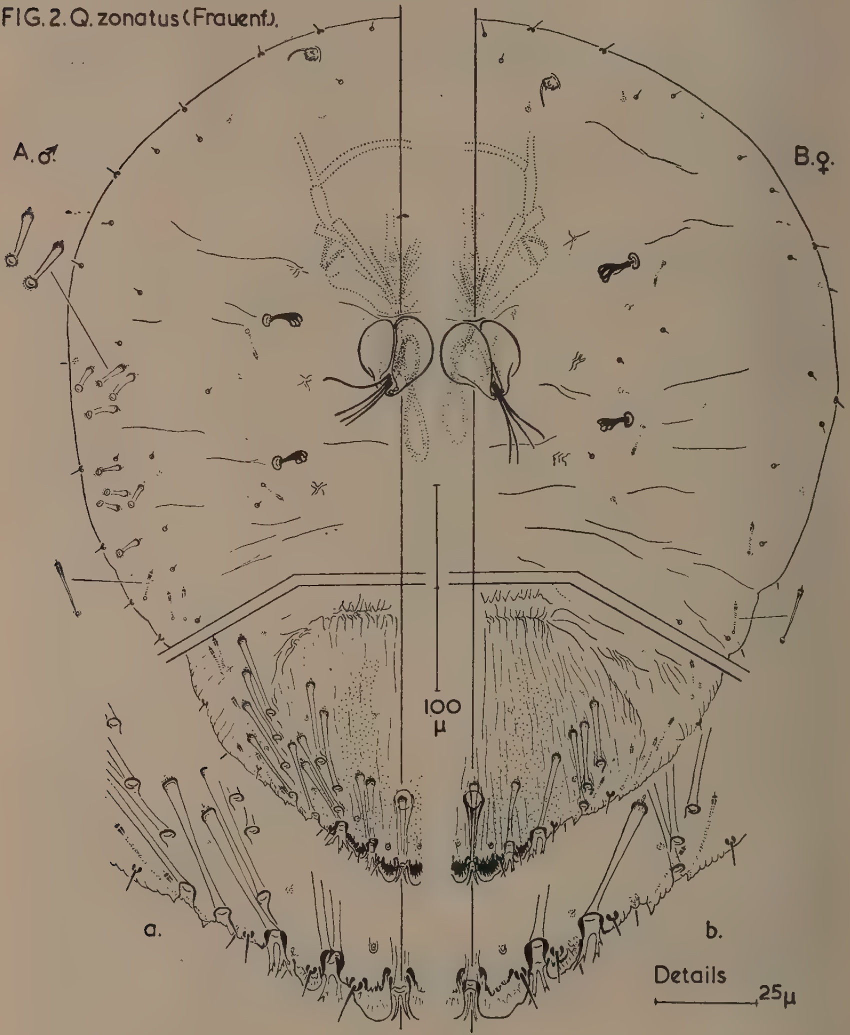
FIG. 2. Q. zonatus (Frauenf).

FIG. 2.—*Quadraspidiotus zonatus* (Frauenfeld). A, male ; B, female ; anterior part of the body in ventral aspect, pygidium in dorsal aspect. *a*, *b*, marginal details of pygidium of male and female, respectively, in dorsal aspect. Details of the respective opposite sides in dotted lines.

but may, and usually does, vary on the two sides of the same insect.[8] The marginal series of *short macroducts* characteristic of the male is composed of 2 ducts in mesothorax, 2 (occasionally 3, average 2·2) on metathorax and one on 1st abdominal segment; no ducts of this type encountered in female. *Microducts:* marginal series extending from mesothorax to 6th abdominal segment, segments 4–6 (pygidial) each with 2–5 ducts in marginal or submarginal ventral group, prepygidial segments each with 1–3 ducts scattered over wide marginal area. Subventral and subdorsal series irregular, often incomplete in male and considerably reduced in female. A few microducts scattered on head and sternal area of thorax.

(3) *Quadraspidiotus zonatus* (Frauenfeld). Specimens from *Quercus robur.*

The *scales* produced by the 2nd instar male and female are similar in texture, but differ in volume, the female scale being considerably thinner. The *body* is broadly oval in both sexes at first, but later the male becomes elongate, the female circular; both of about the same length when fully grown.

Microscopic structures (fig. 2).—*Segmentation* of body obscure in both sexes, especially in individuals advanced in growth. *Pygidium* relatively very large, composed of 4th and following segments, well sclerotized, except for partly membraneous 4th segment. Within the pygidium two pairs of sclerotized areas; the median pair elongate, beginning at base of median lobes and diverging anteriorly; the lateral pair shorter and oblique, beginning around base of second lobes. *Body setae:* marginal, submarginal ventral and subventral series well developed; subdorsal reduced to short longitudinal row composed of three setae apparently belonging to mesothorax, metathorax and 1st abdominal segment. *Antennae* short, cylindrical rugose tubercles with one subapical curved seta. *Spiracles* equidistant from mid-line and margin, with bar enlarged and reticulate at median end. *Eyes* very inconspicuous, simple convex sclerotizations in male; not observed in female. *Labium* large, conical. *Anal opening* small, its diameter about the length of median lobes at a distance of about 2·5 times this diameter from the posterior apex. *Marginal structures* of pygidium similar in both sexes. *Lobes*, two sclerotized pairs; in male appreciably smaller; median lobes prominent, straight, proximate with their outer margins shallowly notched; second lobes small, with sloping outer margin. Third lobes indicated by minute sclerotized points. *Marginal setae* relatively small and short, subequal to length of lobes. *Plates* small; difficult to observe on some otherwise perfect mounts. A pair of very slender simple plates between median lobes; two slender, shallowly bifid or trifid plates between median and second lobes; two secondarily subdivided plates between second lobe and setae of 6th segment, the more lateral plate often very deeply bifid. No microducts associated with these plates. Beyond the setae of 6th segment one or two small membraneous prominences, each with the opening of a microduct at base. *Macroducts*, " one-barred ": *long* pygidial *macroducts* arranged in groups and rows, the females showing markedly fewer ducts in groups and absence of some rows. Between median lobes a single duct with its inner end reaching the anal opening; between median and second lobes a marginal cluster of 2–3 ducts (average 2·1) in male, but a single duct in female; between second lobe and setae of 6th segment, one marginal duct in both sexes and a short row of 3–4 ducts (average 3·1) opposite it in male, and none in female; between setae of 6th and 5th segments, in the male, two marginal ducts arranged in a line parallel to margin and opposite the more lateral duct a longitudinal row of 3–4 ducts (average 3·1); in female, only one marginal duct and 1–2 ducts (average 1·5) opposite it. No macroducts on 4th segment of either sex. Thus, in male there are 11–13, and in female only 4–5 ducts on

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[8] The figures given refer to the specimens from *Betula alba*. Thiem and Gerneck (1934) have shown that in the 2nd instar female of this species the numbers of ducts differ in specimens from different host-plants. Different numbers of ducts in the groups are also shown in Ferris's drawing of intermediate female based on specimens from apple (Montana) and plum (Utah) (Ferris, S.II. 258).

each side of the pygidium. *Marginal* series of *short macroducts* characteristic of male is composed of 3–5 ducts (average 4·0) on mesothorax, 3–4 (average 3·5) on metathorax, and 1 duct on 1st abdominal segment. *Microducts* few: marginal series extending from 2nd

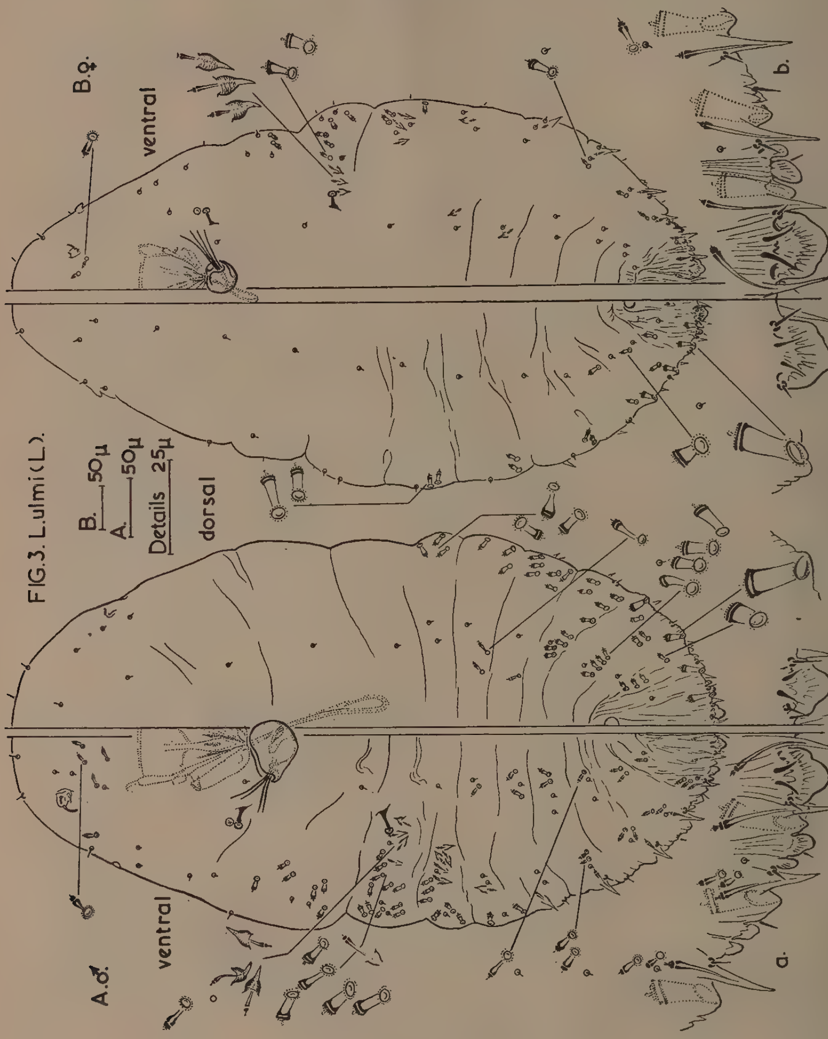

Fig. 3.—*Lepidosaphes ulmi* (L.). A, male; B, female; half ventral and half dorsal aspect. *a*, *b*, marginal details of the pygidium of the male and female, respectively, in ventral aspect, with details of the opposite side in dotted lines.

to 6th abdominal segments, the 5th and 6th each carrying 2–3 ducts, and the preceding three segments each with 1 microduct in female, and 1–2 in male. Subventral and subdorsal series missing in both sexes. Two or three microducts on each side of the sternal area of thorax, usually one near each spiracle.

DIASPIDINI.

(4) *Lepidosaphes ulmi* (L.). Specimens from *Calluna vulgaris.*

The *scales* produced by the 2nd instar male and female are of the same texture, but differ in volume, that of the female being noticeably thinner. At a later stage of growth the female scale becomes broadly pyriform, enlarged posteriorly, and the male " puparium " elongate, narrow, similar to the scale of adult female, but considerably smaller. Shape and size of *body* identical in both sexes immediately after the first moult ; later the male becomes elongate and parallel-sided, while the female becomes pyriform, broadened posteriorly. When fully grown the female is about 1·5 times the length of the male.

Microscopic structures (fig. 3).—*Segmentation* of body distinct, especially in the male. Pygidium small, in both sexes composed of 6th and following segments, fused and sclerotized. *Body setae :* all series well developed, complete and distinct in both sexes ; the subventral, on 4–6 abdominal segments, composed of two setae on each segment instead of the usual one. *Antennae* short, cylindrical tubercles, with one stout curved apical seta and apparently two shorter ones laterally. *Spiracles* equidistant from mid-line and margin ; with narrow bar enlarged at median end ; anterior spiracle with 1–2 disc pores immediately in front of spiracular opening. *Eyes* small, simple, slightly convex sclerotizations in male ; in female in form of small eye-tubercles, but on some mounts globular, or obscure. *Labium* conical with round base. *Anal opening* small, its diameter about half width of median lobes, at the distance of about this diameter from anterior margin of pygidium. *Marginal structures* of pygidium similar in both sexes. *Lobes,* two sclerotized pairs, appreciably smaller in male ; median pair well developed, large, distinctly separated, each with margin shallowly notched on both sides ; second lobes smaller, bilobed, more median lobule larger ; third lobes : in female, absent or indicated by membraneous bilobed prominences, in male the bilobed prominences more distinct, occasionally sclerotized and similar to second lobes. *Marginal setae* of pygidium small, with two dorsal and one ventral setae at base of each median lobe. *Gland spines* large and conspicuous in both sexes ; a pair between median lobes, and 6 on each side of pygidium (segments 3–8 each with one spine). *Gland tubercles* well developed in both sexes, in subventral clusters on metathorax (3 tubercles in female, 4 in male), 1st abdominal segment (3 in female, 3–5 in male) and 2nd abdominal segment (1 tubercle in both sexes) ; one or two tubercles occur irregularly on anterior urosternites of female. *Glandular system :* (1) *Large macroducts* normally developed in both sexes, in a single marginal row composed of 4 ducts, segments 4–7 each with one duct which opens on a prominent marginal gland spur. (2) *Smaller macroducts* in longitudinal series complete in male, somewhat reduced in female. (A) *Marginal series :* on mesothorax a group of 1–3 ducts in female and 5–7 in male, average 2·2 and 6·1 respectively ; on metathorax a wide transverse band extending from margin towards spiracle, composed of 4–6 ducts in female and 10–14 in male (average 4·9 and 12·1 respectively) ; on 1st abdominal segment, 4–6 ducts in female and 9–11 in male (average 5·1 and 9·0 respectively) ; 2nd and 3rd abdominal segments each with 2 ducts in female and 4–7 in male. Posterior section of this series on 4th and following segments subdivided into two longitudinal bands or rows : (*a*) submarginal ventral, in female a single irregular row on segments 4–6, each segment with one duct (range 0–2, average 1·1), and in male a double row on segments 4–7, each segment with 2 ducts, (*b*) submarginal dorsal, in female a single irregular row on segments 4–6, each segment with one duct (range 0–2, average 0·9), and in male a series of gradually smaller clusters of ducts on 4th (about 5 ducts), 5th (2–3 ducts) and 6th (1–2 ducts) abdominal segments. (B) *Subventral* series missing in female ; in male represented by a double row on segments 2–7, each segment with 2 ducts. (C) *Subdorsal* series reduced in female to a short row on segments 4–6, each segment with one duct ; in male it extends from 4th to 6th abdominal segments, each segment with 2–4 ducts (average 3·0) in a transverse row, thus forming a short but wide longitudinal subdorsal band. A few ducts scattered on ventral area of head, 1–3 ducts in female and 4–6 in male. *Microducts* always associated with gland spines and gland tubercles, the former being considerably longer.

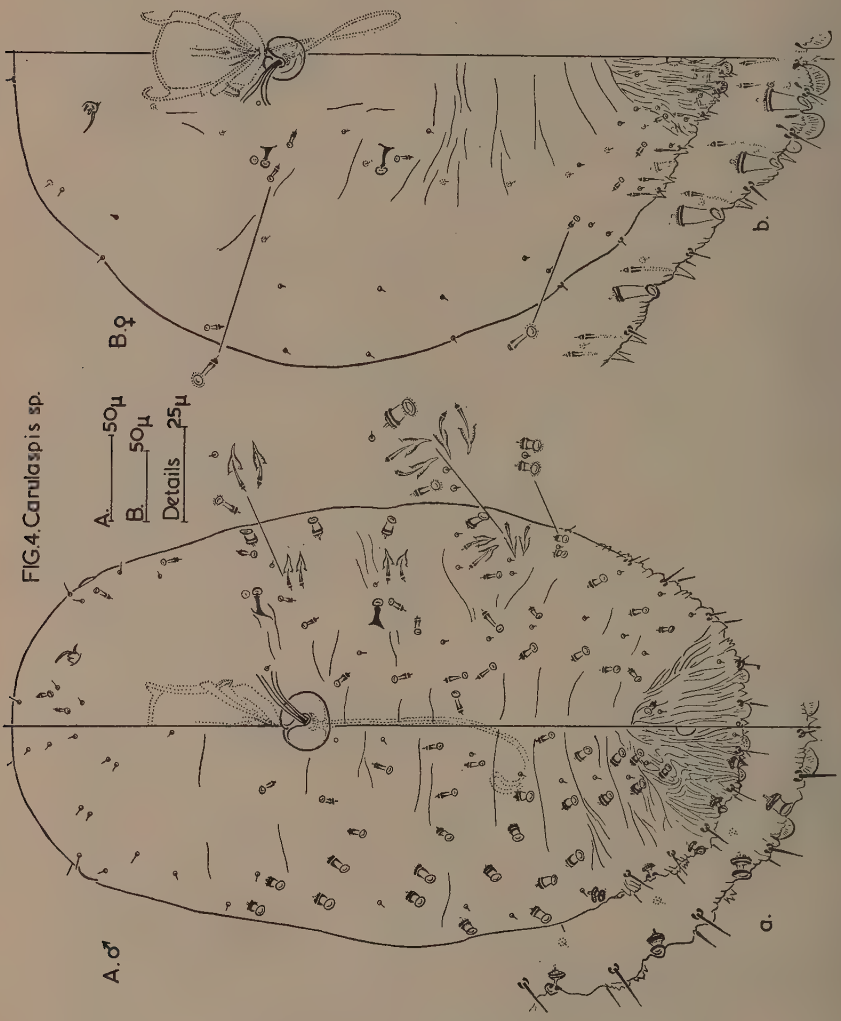

FIG. 4.—*Carulaspis* sp. A, male, half dorsal and half ventral aspect; B, female, half of the body in ventral aspect, with details of the opposite side in dotted lines. *a*, *b*, marginal details of pygidium of male and female, respectively, in dorsal aspect. Details of the opposite side in dotted lines.

(5) *Carulaspis* sp. Specimens from *Juniperus sinensis*.

The *scales* produced by the two sexes in the 2nd instar show characteristic differences as soon as they are secreted, the female scale being oval, smooth, thin and colourless, and the male "puparium" elongated, tricarinate, somewhat felted, thick and white. The *body* of both sexes is identical at first, the female later becoming broadly pyriform, with considerably enlarged anterior end, and the male stout and elongate.

Microscopic structures (fig. 4).—*Segmentation* of body obscure in female ; in male rather distinct, with submarginal ventral areas of 1st and 2nd abdominal segments apparently fused. *Pygidium* developed in both sexes, composed of 6th and following segments, sclerotized ; sclerotization somewhat heavier in female. *Body setae* in the usual longitudinal series, complete in male, in female subventral series missing on anterior urosternites. *Antennae* short, rugose tubercles, with one long curved apical and 1–2 smaller lateral setae. *Spiracles* equidistant from mid-line and margin in male, nearer to mid-line in fully grown female ; anterior spiracles with one disc pore. *Eyes* simple, convex sclerotizations in male, in female not observed. *Labium* globular. *Anal opening* in both sexes relatively large, its diameter about the width of median lobes ; situated slightly posterior to centre of pygidium. *Marginal structures* of pygidium differ in some details in the two sexes. *Lobes :* two pairs developed, those of male conspicuously reduced : median lobes rounded, well separated, in female longer than wide, in male their length about half the width ; second lobes deeply bilobed, median lobule much larger, in female both lobules sclerotized, in male the more lateral only slightly sclerotized or not at all. *Marginal setae* well developed in both sexes, more conspicuous in male. *Gland spines* present only in female, comparatively stout ; between median lobes a pair, or a single forked spine with two microducts and 6 other spines on each side of pygidium, segments 5–8 each with one, and 4th segment with 2 spines. In male no gland spines and no microducts, the margin of pygidium between lobes and beyond second lobes irregularly serrate, some of the membraneous prominences somewhat resembling the fimbriate form of pygidial plates. *Gland tubercles* absent in female ; in male in usual subventral groups on mesothorax (2 tubercles), metathorax (2 tubercles) and on fused submarginal area of 1st and 2nd abdominal segments (4 tubercles). *Glandular system* differs considerably in the two sexes. (1) *Large macroducts* on margin of pygidium : in female normally developed, four on each side in marginal row, segments 4–7 each with one duct ; in male 5 modified ducts on each side of pygidium, posteriormost (between median and second lobes), although very short still resembling tubular form, the preceding four (on segments 3–6) showing increasing degree of modification towards cup-like pores, the anteriormost (on 3rd segment) submarginal in position, with characteristic kidney-shaped external opening. (2) *Smaller macroducts :* In female the number considerably reduced, to 3–4 ducts in a single submarginal ventral row on segments 3–6 or 4–6, each segment with one duct, and a very few ducts scattered on sternal area of thorax and on margin of prothorax. In male these ducts numerous, in more or less complete series : (A) *Marginal series* on wide marginal area of mesothorax, metathorax and 1st–3rd abdominal segments, each with 3–4 ducts arranged in an oblique row ; posterior section of this series represented by a single submarginal ventral row on segments 4–6, each segment with one duct ; the submarginal dorsal branch absent. (B) *Subventral series* forms an irregular, partly double row on abdominal segments 1–7, and (C) *Subdorsal series* extends from mesonotum to 6th abdominal segment, each segment with 1–3 (usually 2) ducts forming a wide longitudinal band partly coalescent with marginal series. A few smaller macroducts scattered on sternal area of thorax and along anterior margin of cephalothorax. *Microducts* associated with pygidial gland spines in female, and gland tubercles in male ; no microducts on margin of pygidium in male.

(6) *Chionaspis salicis* (L.). Specimens from *Tilia* sp.

The *scales* produced by the 2nd instar of the two sexes differ, the female scale being smooth and thin, the male " puparium " strongly tricarinate, felted and thick. The size and shape of the *body* are similar at first ; the female later becomes pyriform, widest at posterior half, and the male stout and elongate. In the male the cephalothorax is longer than the abdomen, in the female shorter; when fully grown the female is about 1·5 times the length of male.

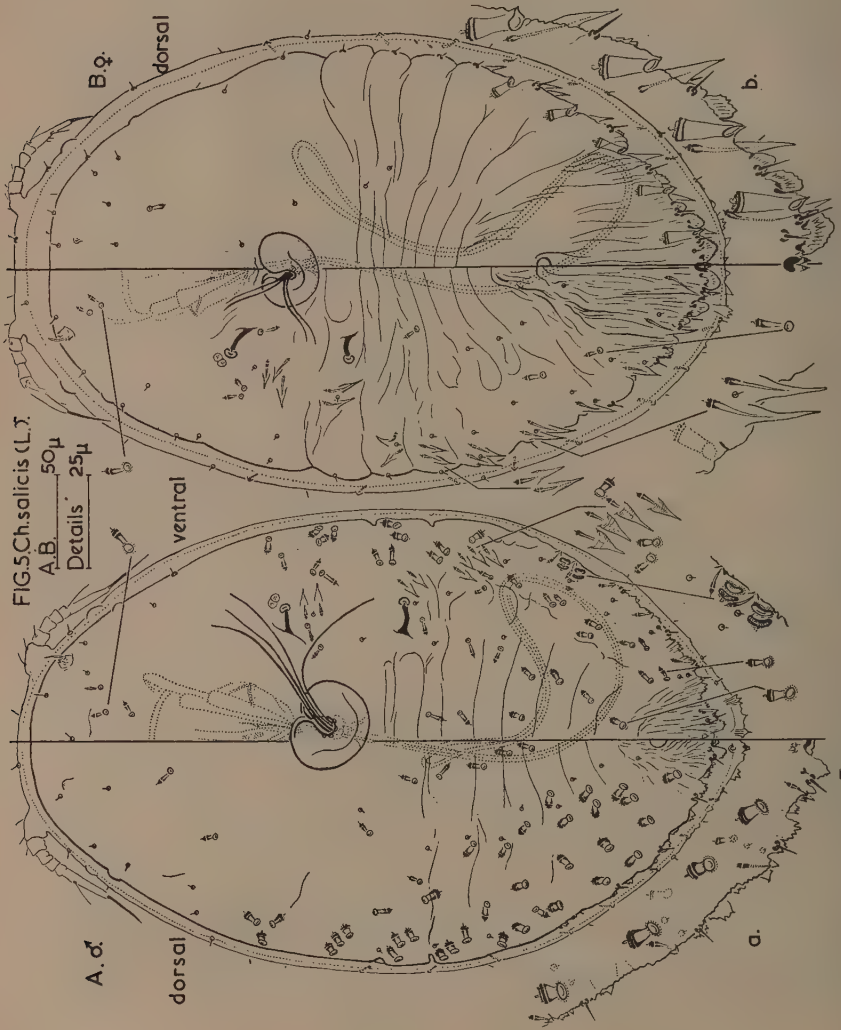

Fig. 5.—*Chionaspis salicis* (L.). A, male; B, female; half ventral and half dorsal aspect; the specimens immediately after the first moult and still enclosed within the skin of the first larva drawn in outline. *a*, *b*, marginal details of the pygidium of the male and female, respectively, in dorsal aspect.

Microscopic structures (fig. 5).—*Segmentation* distinct on prepygidial part of abdomen; in male the submarginal ventral areas of 1st and 2nd and of 3rd and 4th segments fused. *Pygidium:* In female large, composed of 6th and following segments, fused and sclerotized, with anterior margin reaching one-third length of newly moulted 2nd instar; prepygidial segments arched and folding around pygidium. In male small, composed of 7th and following segments, fused and slightly sclerotized, with anterior margin reaching about one-seventh length of newly moulted 2nd instar. *Body setae* in usual longitudinal series except that in male, abdominal section of subventral row irregular and incomplete, and in female, abdominal part of subdorsal row absent. *Antennae* small, rugose tubercles, with one long curved apical seta. *Spiracles :* in female more median, in male more lateral ; anterior spiracles with 1–3 disc pores. *Eyes* small, convex sclerotizations in both sexes. *Labium* large, globular. *Anal opening*, the same size in both sexes, about half width of median lobes of female, situated in female at about 10 times its diameter from posterior apex and in male at 3 times this diameter. *Marginal structures* of pygidium differ in the two sexes. *Lobes :* in female well developed, sclerotized ; median lobes large, zygotic with sclerotized yoke, oblique median margin forming apical notch ; second lobes bilobed, both lobules sclerotized, the more lateral smaller ; third lobes bilobed, median lobule slightly sclerotized, lateral membraneous. In male no sclerotized lobes, pygidial margin with numerous irregular membraneous prominences, position of marginal setae apparently indicating that the larger prominences correspond with pygidial lobes of female. *Marginal setae :* usual series present in both sexes. *Gland spines :* in female normally developed, long, in continuous longitudinal series from mesothorax to 8th abdominal segment, segments 5–8 each with one marginal spine, segments 1–4 each with 2 submarginal ventral spines, metathorax and mesothorax each with subventral group of 2 and 3 spines respectively. In male, gland spines reduced to small conical " raised glands " on margins of 3rd–8th abdominal segments each segment with one gland. No gland spines and " raised glands " between median lobes in female nor in corresponding position in male. *Gland tubercles :* in male, rather slender. approaching the form of spines, but slightly sclerotized, in the usual three subventral groups on mesothorax (2–3 tubercles), metathorax (2 tubercles) and on fused submarginal ventral area of 1st and 2nd abdominal segments (4 tubercles). In female, corresponding positions occupied by gland spines. *Glandular system* of the two sexes differs considerably. (1) *Large macroducts* on margin of pygidium : In female normally developed, 5 ducts on each side of pygidium, in marginal row, segments 3–7 each with one duct. In male absent, except two modified cup-like ducts on fused submarginal ventral area of 3rd and 4th abdominal segments. (2) *Smaller macroducts :* in female, the number considerably reduced to 3 or 2 ducts in submarginal ventral row on segments 4–6 or 5–6, each segment with one small duct, an occasional single duct on anterior urosternites and a few scattered on sternal part of thorax and on head. In male, numerous, forming complete longitudinal series : (A) *Marginal series* composed of ducts scattered or arranged in irregular oblique rows over wide marginal area of mesothorax (9–13 scattered ducts, average 10·8), metathorax (7–10 ducts, average 8·2, in irregular oblique band), and on fused marginal area of 1st and 2nd abdominal segments (7–12 scattered ducts, average 8·3) ; posteriorly the submarginal ventral and the submarginal dorsal branches of this series are represented by partly double rows on 3rd–7th abdominal segments. (B) *Subventral series*, in form of a single row on 2nd–7th abdominal segments, each segment with one duct ; additional longitudinal row of 2–3 ducts near mid-line on anterior urosternites. (C) *Subdorsal* series, in form of partly double row on 1st–6th abdominal segments, each segment usually with 2 ducts ; additional longitudinal row of 4–5 ducts close to mid-line on anterior urotergites. A few ducts scattered on sternal area of thorax and on head. *Microducts* associated with gland spines in female and with raised glands and gland tubercles in male ; microducts of pygidial gland spines of female considerably longer.

(7) *Aulacaspis rosae* (Bouché). Specimens from garden rose, *Rosa* sp.

The scales produced by the 2nd instar differ distinctly in the two sexes, that of the female being smooth, thin and transparent, and the male "puparium" strongly tricarinate, felted, white and thick. The size and shape of the *body* are similar at first, but in the male the cephalothorax is longer than the abdomen and in the female shorter ; the growing female becomes enlarged and somewhat cylindrical anteriorly with narrowing posterior end; the male becomes stout and elongate with slightly enlarged posterior half. When fully grown both sexes are of about the same length.

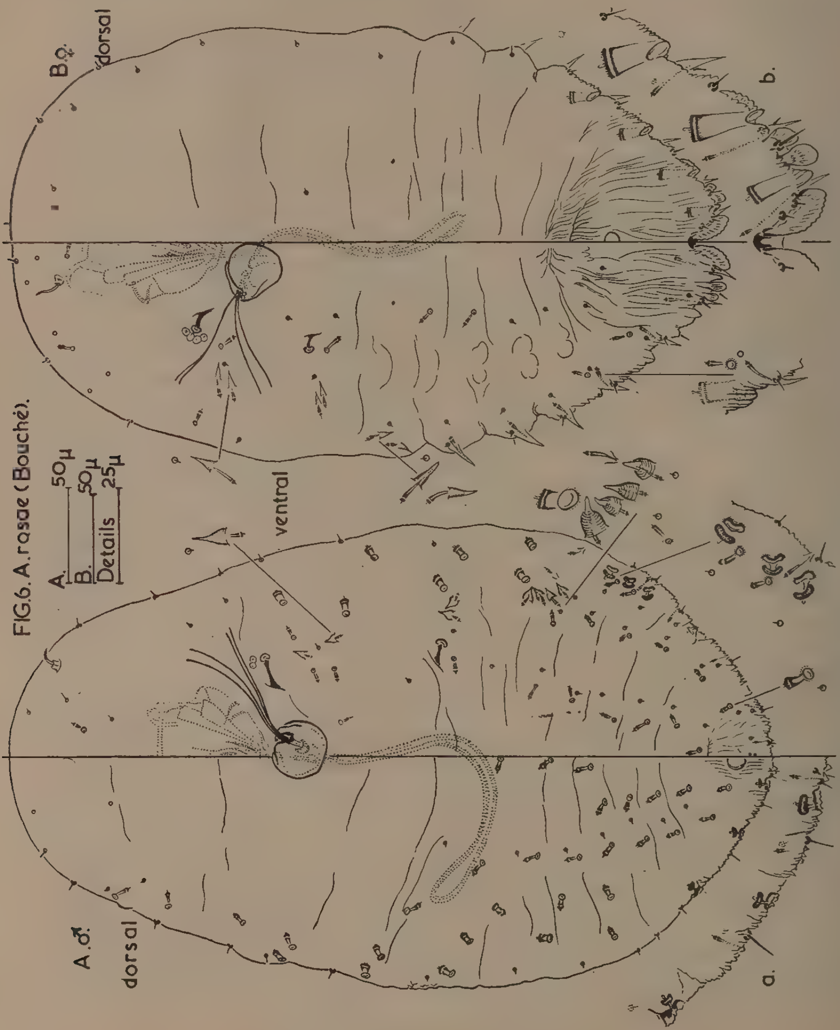

Fig. 6.—*Aulacaspis rosae* (Bouché). A, male; B, female; half ventral and half dorsal aspect. *a*, *b*, marginal details of pygidium of male and female, respectively, in dorsal aspect.

Microscopic structures (fig. 6).—*Segmentation* of body distinct on abdomen, obscure on cephalothorax; in male the submarginal ventral areas of 1st and 2nd and of 3rd and 4th abdominal segments fused. *Pygidium:* in female large, composed of 6th and following segments fused and sclerotized, anterior margin reaching ¼ length of young insect. In male, pygidium practically absent, 7th and following segments fused but membraneous, except for small slightly sclerotized area around anal opening. *Body setae* in usual longitudinal series, except that in female, abdominal section of subdorsal series absent and subventral series incomplete, and in male, subdorsal series limited to abdominal segments only. *Antennae* small, rugose tubercles with one long curved apical seta. *Spiracles :* anterior one relatively nearer mid-line and with 2–4 disc pores. *Eyes* small, simple convex sclerotizations in male ; in female, not observed. *Labium* stout, conical with round base. *Anal opening* small, the same size in both sexes, its diameter about half width of median lobes of female, situated in female at about 4 times this diameter from posterior apex and at less than twice this diameter in male. *Marginal structures* of pygidium differ considerably in the two sexes. *Lobes :* in female, two pairs, well developed, sclerotized ; median lobes large, with yoke, median margin serrate and oblique, forming apical notch ; second lobes bilobed, both lobules sclerotized ; third lobes obscure, the apparently median lobule wide but short, sclerotized, and the lateral one in the form of raised membraneous prominence. In male, lobes absent, the whole posterior margin of abdomen membraneous, with small irregular marginal serrations. *Marginal setae :* usual series in both sexes, setae smaller in male. *Gland spines :* in female, normally developed, long, in continuous longitudinal series from mesothorax to 8th abdominal segment, segments 2–8 each with one marginal spine, 1st abdominal segment, metathorax and mesothorax each with 2 subventral or submarginal ventral spines. In male, gland spines reduced to small conical " raised glands," segments 2–8 each with one gland. No gland spines or raised glands between median lobes in female nor in corresponding position in male. *Gland tubercles :* in male, of typical form, stout and slightly sclerotized, in usual three subventral groups on mesothorax (2 tubercles), metathorax (2 tubercles) and on fused submarginal area of 1st and 2nd abdominal segments (4 tubercles). In female, corresponding positions occupied by gland spines. *Glandular system* of the two sexes differs considerably. (1) *Large macroducts* on margin of pygidium : in female, normally developed, four on each side of pygidium in marginal row, segments 4–7 each with one duct. In male, modified into cup-like pores, six on each side, segments 5–7 each with marginal duct and a submarginal ventral group of 3 ducts on fused area of 3rd and 4th segments. (2) *Smaller macroducts :* in female, the number reduced to two submarginal ventral ducts, one each on segments 5 and 6, one or two subventral on anterior urosternites, and a few scattered ducts on sternal part of thorax and on head. In male, ducts numerous, forming more or less complete series : (A) *Marginal series*, on wide marginal area on mesothorax (4–7 scattered ducts), metathorax (4–5 ducts in an oblique row), and on 3 anterior abdominal segments (each segment with an oblique row, composed of 4–6 ducts on 1st, decreasing to 2–3 ducts on 3rd segment) ; posteriorly the submarginal ventral branch of this series represented by single longitudinal row reaching 7th segment and the submarginal dorsal branch is missing. (B) *Subventral series*, a single row on 2nd–7th abdominal segments, each segment with one small duct. (C) *Subdorsal series*, a partly double row on segments 1–7, each usually with 2 ducts ; additional longitudinal row composed of 3 small ducts, close to mid-line, on anterior urotergites. A few small ducts scattered on sternal area of thorax and on antero-lateral margin of head. *Microducts*, associated with gland spines in female and with gland tubercles and raised glands in male ; microducts of pygidial gland spines of female considerably larger.

IV. CONCLUSIONS.

The following conclusions refer to 15 species and are drawn from observations on the seven species here described (p. 453) and from the information available for the other 8 species (foot-notes 1–5, p. 452). The postembryonic development of these species comprises 3 instars in the female and 5 instars in the male, the latter including 2 larval instars, 2 pupal and the imago.

(1) All these species show sexual dimorphism in 2nd (larval) instar, but the degree of differentiation varies considerably in the different species. The

relevant characters concern (*a*) the glandular system and (*b*) the development of the pygidium.

(*a*) Sexual dimorphism in the development of the glandular system is shown in the different numbers of ducts, often of different types, and, occasionally, in the different sizes of some ducts in the two sexes. The female 2nd instar has fewer ducts, often fewer types of ducts, and, if there is any difference in the size, the ducts of the female are smaller. The relative reduction of the glandular system of the female in this instar, although at times very small, seems to be the only general feature which applies to all known instances.

(*b*) The pygidium and the marginal details of the pygidium are either well developed in both sexes, or are reduced in the male. The pygidium of the 2nd instar female is always well developed, being similar to that of the adult female and showing some of the specific and generic characters of the latter. The pygidium of male 2nd instar of some species is similar to that of the 2nd instar female, except for the slightly smaller size of the lobes. In some other species, however, the pygidium of the male is more or less reduced, or not developed at all.

(2) The species here discussed can be tentatively arranged into groups, each with a characteristic type of sexual dimorphism, namely: (*a*) species of the tribe Aspidiotini, (*b*) species of the genus *Lepidosaphes*, and (*c*) the four other species (and genera) of Diaspidini (*Carulaspis*, *Chionaspis*, *Aulacaspis*, *Epidiaspis*). No specimens of *Parlatoria* or related genera were studied by the author and a discussion of them is therefore omitted, though it appears that they may form a separate group with a different type of sexual dimorphism and with variable conditions even within the genus *Parlatoria* (cf. Berlese, 1896, for *P. zizyphus* (Lucas), and Stickney, 1934, for *P. blanchardii* (Targ.)).

(*a*) *The type apparently characteristic of the species of Aspidiotini.* Here the relevant feature distinguishing the two sexes in the 2nd instar is the marginal series of short but comparatively wide macroducts (" pori marginali "—Lombardi, 1938) which occur on the mesothorax, metathorax and 1st abdominal segment of the male but are absent in the female. These conditions were found in all three species studied by the author (*Diaspidiotus bavaricus*, *Quadraspidiotus ostreaeformis*, *Q. zonatus*), and in *Targionia vitis* described by Lombardi (*l.c.*). Unfortunately there is no information on this point in the other three species studied by Berlese (l.c.). In all seven species the pygidium is well developed and similar in both sexes, except for the smaller size of the pygidial lobes in the male. In *D. bavaricus* and *Q. ostreaeformis* the numbers of the pygidial ducts are very similar in both sexes, but in *Q. zonatus* and *T. vitis* there are fewer of these ducts in the female. Conditions similar to the latter are apparent from a comparison of Berlese's drawings and descriptions of the male 2nd instar with Ferris' drawings of the 2nd instar female in *Aspidiotus hederae*, *Chrysomphalus ficus* and *Aonidiella aurantii*. In *T. vitis* some pygidial macroducts of the female are somewhat smaller than those of the male.

(*b*) *The type found in* Lepidosaphes ulmi.—Here sexual dimorphism is shown in the different numbers of smaller macroducts, the series of these ducts being somewhat reduced and composed of fewer ducts in the female. Otherwise the two sexes are very similar, both having the same types of ducts and other structures (gland spines, gland tubercles), and the pygidium is equally well developed and similar in the two sexes, except for slightly smaller pygidial lobes in the male. Similar conditions were found in *L. tuberculata* Malen., and are apparent from Berlese's descriptions and drawings of *L. beckii.*

(*c*) *The type found in* Carulaspis *sp.*, Chionaspis salicis, Aulacaspis rosae *and* Epidiaspis leperii.—In these species sexual dimorphism is rather variable in details. The common features are shown in the condition of the marginal pygidial ducts, and in the relative numbers of the smaller macroducts in the two sexes. In the female the marginal pygidial ducts are of the normal tubular form and are arranged in a single marginal row characteristic for Diaspidini. In the male these ducts are modified into cup-like pores (" pores à cupule "—Geier, 1949) occurring in full (*Carulaspis* sp., *A. rosae*, *E. leperii*), or reduced (*C. salicis*) numbers, and often forming a particularly conspicuous group on the fused submarginal ventral area of the 3rd and 4th abdominal segments (*A. rosae*, *C. salicis*). The smaller macroducts are always numerous in the male and reduced to a very few in the female. The pygidium, pygidial lobes and gland spines are always present and well developed in the female, the spines occurring either on the margin of the pygidium only (*Carulaspis* sp.), or forming a continuous longitudinal marginal series from the mesothorax to the 8th abdominal segment (*C. salicis*, *A. rosae*), and the gland tubercles are absent in the female. In the male, on the other hand, the pygidium and pygidial lobes may be still present, although much less sclerotized than in the female (*Carulaspis* sp.), or the pygidium is reduced in size with the lobes membraneous (*C. salicis*), or both the pygidium and the lobes are absent (*A. rosae*). The gland spines on the margin of the pygidium of the male are reduced to " raised glands " (*C. salicis*, *A. rosae*), or absent (*Carulaspis* sp.), and the gland tubercles are always present in the three subventral groups on the mesothorax, metathorax and the fused submarginal ventral area of the 1st and 2nd abdominal segments.

(3) It appears that in so far as the development of the glandular system, and especially the number of macroducts is concerned, the 2nd instar male generally resembles the adult female more than does the 2nd instar female. Should the development of the glandular system be taken as a measure of ontogenetical development, the 2nd instar male would appear to be more advanced than the 2nd instar female, and so occupy a position intermediate between the 2nd instar female and the adult female. Börner's suggestion of a close correspondence between the 3 larval instars of the male and the 3 instars of the female resulted from confusion of the larval instars in the male series of *A. rosae* (see page 453).

(4) The sexual differences in anatomical structures are apparently reflected in differences in the texture and volume of the scales secreted by the 2nd instar larvae of each sex. The texture seems to depend on the development of the pygidium and its marginal structures, while the volume depends on the number of macroducts. In *D. bavaricus* and *Q. ostreaeformis* (in which both sexes in this instar have well developed pygidia and similar numbers of pygidial ducts) the scales produced by the male and female insects are similar in both texture and volume. In *Q. zonatus* and *L. ulmi* (in which the pygidium is well developed in both sexes, but the number of ducts is reduced in the female) the female and

male scales are similar in texture but differ in volume, the female scale being thinner. In *Carulaspis* sp., *C. salicis* and *A. rosae* (in which the male has the pygidial structures reduced or absent and the number of macroducts in the female is considerably reduced) the scales produced by the two sexes differ markedly in both texture and volume.

(5) In respect of the condition of the glandular system, which in this instar is always well developed in the male, and often considerably reduced in the female, the male "puparium" is always comparatively thick and conspicuous, while the female scale is often very thin and inconspicuous. This fact has some bearing on the relative permanence of the scales secreted by the two sexes in this instar. The scale secreted by the 2nd instar male represents the permanent and final "puparium" under which the development of prepupa, pupa and imago takes place with no further addition of secretory matter at those subsequent stages. In the female the scale produced by the 2nd instar is transitory, the final scale being completed by the adult female. Perhaps this fact would also support the view that the male in the 2nd instar is more advanced and, so far as the completion of the scale is concerned, corresponds rather with the adult female.

(6) In *D. bavaricus* and *Q. ostreaeformis* the similarity of the anatomical details and, subsequently, of the well developed and equally voluminous scale secreted by the two sexes in this instar, coincides with similar life cycles which in both species involve hibernation of the male and female insects in the 2nd instar. In the other five species studied the 2nd instar female has a reduced number of macroducts and secretes a thin or very thin scale. With the exception of *A. rosae*, all these species complete their development before the winter sets in and hibernate either as eggs (*L. ulmi*, *C. salicis*), or as young adult females (*Q. zonatus*, *Carulaspis* sp.). *A. rosae*, although during the season of observation (1949–50) was observed to hibernate in the 2nd instar, has in fact a very irregular life cycle in Great Britain, and apparently can survive only in well sheltered positions. It is interesting to note that in France (in the Paris area) both *A. rosae* and *Q. ostreaeformis* have similar life cycles, both completing their development before the winter and hibernating as adult females (Balachowsky and Mesnil, 1936, **II**). But in Great Britain the latter species is well established, with a regular life cycle, while the former is not. Apart from specific physiological reactions determining the success of each species in different climates, these observations would suggest some correlation between the anatomical conditions (and the resulting character of the waxy scales) and the successful survival of the species in cooler climates. The available information, however, is at present insufficient for any generalization.

(7) The arrangement of pygidial ducts into groups and rows in the 2nd instar of the species of Aspidiotini studied appears to be constant and characteristic for each species, and the number of ducts in each group is constant within certain well-defined ranges. The latter observation is probably due to the fact that the specimens of each species studied were taken from one host-plant species only. Thiem and Gerneck (1934) have shown that in the 2nd instar female of *Q. ostreaeformis* the numbers of ducts in groups, although more or less constant in specimens from any particular host-plant, vary considerably in specimens from various host plants. The arrangement in groups and rows,

however, seems to be constant, but further detailed studies are necessary to prove that this character can be used for the separation of species, or groups of species in this instar. Such a suggestion is supported by a comparison of the conditions in the three species of Aspidiotini here studied and the conditions in the other 11 species of *Diaspidiotus* and 5 species of *Quadraspidiotus* illustrated by Ferris (1938-1942, S.II. 215–225 ; 256–261).

SUMMARY.

(1) The following seven species of Diaspididae were studied : Aspidiotini : *Diaspidiotus bavaricus* (Lindinger), *Quadraspidiotus ostreaeformis* (Curtis), *Q. zonatus* (Frauenfeld) ; Diaspidini : *Lepidosaphes ulmi* (L.), *Carulaspis* sp., *Chionaspis salicis* (L.), *Aulacaspis rosae* (Bouché).

(2) The postembryonic development of these species comprises 3 instars (including the adult) in the female and 5 in the male, the latter including 2 larval instars, 2 pupal and the imago.

(3) The available information on sexual dimorphism in the 2nd instar of Diaspididae is reviewed.

(4) General observations on the species studied and their life-cycles are recorded ; the uncertainty of the nomenclature of *Carulaspis* sp. is explained.

(5) The morphology of both male and female 2nd instar larvae of each species is described in detail (with detailed drawings of six species).

(6) The following conclusions are drawn from the observations made and from available information.

a. The two sexes at this stage differ to a greater or lesser degree, sexual dimorphism being shown in the relative development of the glandular system and in the condition of the pygidium. The glandular system is always relatively less developed in the female ; in the male of some species the pygidium and pygidial marginal structures are reduced or even absent.

b. Three types of sexual dimorphism are tentatively recognized :

(*i*) the type found in the species of the tribe Aspidiotini, in which a marginal series of prepygidial macroducts is characteristic of the male ;

(*ii*) the type found in *Lepidosaphes* spp., in which the only obvious sexual difference is the lesser number of smaller macroducts in the female ;

(*iii*) the type found in *Carulaspis* sp., *C. salicis*, *A. rosae* and *Epidiaspis leperii*, with some differences in structural details between the species, but with the following features common to all : in the female, a considerable reduction of the number of smaller macroducts ; in the male, the modification of the large marginal pygidial macroducts into cup-like pores and greater or lesser reduction of the pygidium.

c. Sexual differences in structural details are reflected in the different character of the scale of the two sexes, the texture of the scale depending on the development of the pygidium and its marginal structures, and the volume on the number of macroducts.

d. The coincidence of similar degrees of sexual differentiation in *D. bavaricus* and *Q. ostreaeformis* with the similar life cycles of these two species is discussed.

e. The arrangement of the pygidial ducts in groups and rows in the species of Aspidiotini is suggested as a possible character for separation of species in this instar.

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A PRELIMINARY CONTRIBUTION TO THE TAXONOMY OF THE GENERA *HEMIGYMNOCHAETA* AND *TRICYCLEA* (DIPTERA : CALLIPHORIDAE).

By F. Zumpt., Ph.D., F.R.E.S.

(*Dept. of Entomology, South African Institute for Medical Research, Johannesburg.*)

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With 21 Text-figures.

A. Taxonomic Problems.

Hemigymnochaeta Corti (1895) and *Tricyclea* Wulp (1884) are two Calliphorid genera restricted to the Ethiopian region. They contain a fairly large number of small and medium-sized yellow or light brown species which develop in various kinds of organic matter, such as mushrooms, dung and faeces. Other species have been observed to drop their eggs in and between the openings of temporary nests of driver ants, but it is not known if the larvae feed only on the débris or if they have a closer association with the ants (cf. Villeneuve, 1922).

Hemigymnochaeta and *Tricyclea* are so similar in their general appearance that they had been considered as congeneric by Séguy (1933), but later this author separated them again (1946), and the general tendency today is to regard them as distinct units. The main distinguishing feature lies in the propleura, which is bare in *Hemigymnochaeta*, but beset with hairs in *Tricyclea*. Furthermore the thoracic squama is, as a rule, narrow in the former genus and broader in the latter, but this feature does not hold through all the species. The general plan of structure in the phallosomes is the same in both genera, so that the grounds for uniting them as well as for separating them may both be supported by some facts. Mainly for practical reasons, I accept the present status of taxonomy, regarding these two genera as distinct. A synonym of *Hemigymnochaeta* Corti (1895) is *Tricyclodes* Curran (1927), as already considered by Malloch (1929), and a synonym of *Tricyclea* Wulp (1884) is *Zonochroa* Brauer and Bergenstamm (1891), which has been retained as a subgenus by Malloch (1929). The features used by Townsend (1935) for separating these and allied genera are mostly not constant or of any phylogenetic value, so that I refrain from discussing his taxonomy.

The generic features which characterise *Hemigymnochaeta* and *Tricyclea* within the remaining Ethiopian Calliphorinae may be summarised as follows :

Head of male without *v*, *f* and *fo*, *ev* wanting or quite indistinct, frons not wider than one fifth of longest eye-diameter, eyes with large or small upper facets, arista with long hairs on both sides, parafacials bare or with fine hairs, female head with *ev*, *f* and *fo*, mouth parts in both sexes well developed, of *Musca* type. *Thorax* with the propleura haired (*Tricyclea*) or bare (*Hemigymnochaeta*), prosternum haired, alar declivity bare or with a few setae, suprasquamal ridge bare, supraspiracular convexity bare of long hairs, chaetotaxy fully developed, *ph* 2–3, *st* 1 : 1, wing with r_1 bare, r_5 bristled at most up to *r–m*, r_5 open, thoracic squama bare, of different shape; legs without unusual chaetotaxy or features.

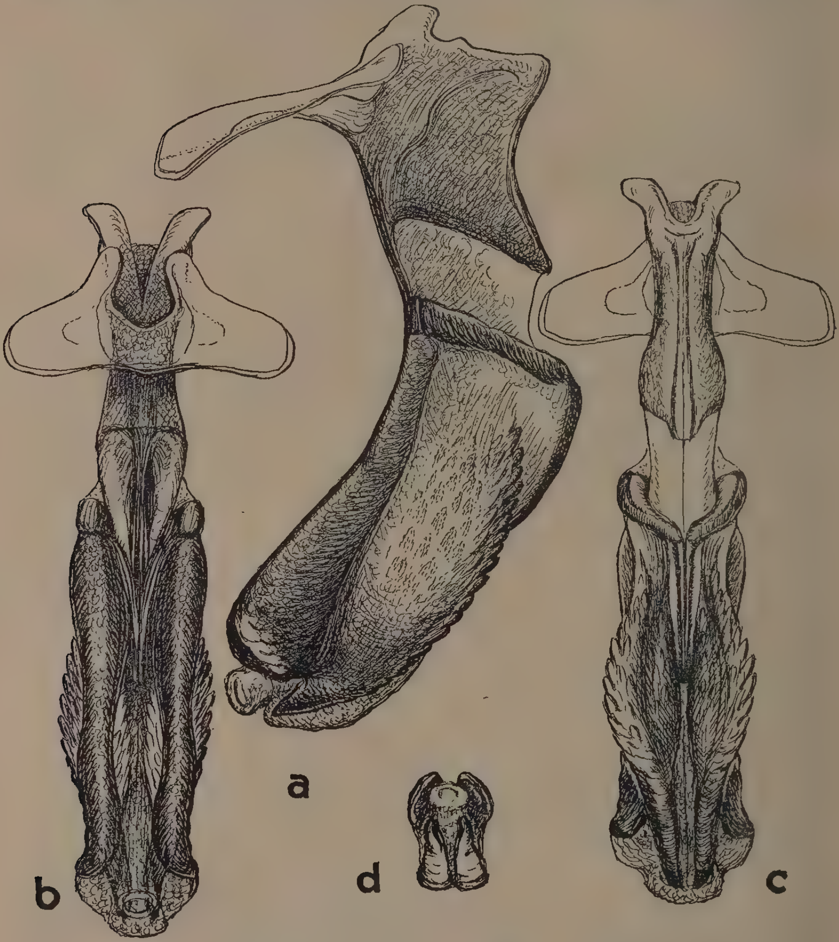

Fig. 1.—Phallosome of *Hemigymnochaeta varia* (Hough). (*a*) Lateral view; (*b*) and (*c*) anterior and posterior view; (*d*) opening of ductus ejaculatorius.

Abdomen with the second sternite large and covering margins of the tergites, the following sternites free, fifth sternite emarginate, with hairs and sometimes with bristles, tergites without median dorsal bristles; hypopygium composed of three free segments excluding the cerci, cerci free, but sometimes close together, paralobi mostly slender, sometimes enlarged, phallosome (fig. 1) with separated theca and phallus, spine present, harpes broad, not spine-like, vesicae consisting of denticulated membranes, general structure of phallosome therefore primitive.

As already mentioned, the only constant feature which can be used to separate *Hemigymnochaeta* from *Tricyclea* is the haired propleura, but the species of *Hemigymnochaeta* are characterised by a few more features which at least are typical for the majority of the members of this genus. The usual shape of the thoracic squama has been discussed. Furthermore, we find that in the *Hemigymnochaeta* there are males with greatly enlarged upper and inner facets of the eyes which are demarcated from the smaller lower ones, but there are also males in which there is no sharp demarcation, but a gradual transition from the larger to the smaller facets. In *Tricyclea*, enlarged facets occur also, but they are transitional to the lower small ones and not sharply demarcated from them. As discussed below, several species of *Hemigymnochaeta* evidently contain several strains which are morphologically quite distinct but are not separated from each other genetically. Such a pronounced intra-specific variability is not known in the *Tricyclea* species, except with regard to the wing pattern. With respect to the structure of the hypopygium, the genus *Hemigymnochaeta* seems to represent the more primitive unit. The cerci and paralobi are slender and of normal shape in all *Hemigymnochaeta* species, whereas in some *Tricyclea* species the paralobi are strikingly enlarged, as in *T. major*, or the cerci may be enlarged as in *T. semicinerea* and *T. patrizii*. Furthermore, the fifth sternite always shows a simple incision in *Hemigymnochaeta*, whereas in a few *Tricyclea* species its shape is unusual and the deep but narrow incision is beset with bristly spines (cf. *T. perpendicularis* and *T. cockbilli*).

The species taxonomy is at present in a very unsatisfactory condition. Most of the former authors based it on external features, e.g. the thoracic chaetotaxy, the width of the frons and the pattern of the wing, mesonotum and abdomen. Only Curran (1927) and Malloch (1929) started to study the male genitalia in order to prove the concept of several doubtful species, but unfortunately they dissected only a few specimens and did not base the whole taxonomy on this organ. I am of the opinion that this feature is diagnostic in these genera, as in other Calliphorids also. This thesis has led me to very interesting and sometimes unexpected results.

As a rule, in both genera the shape of the hypopygium is very characteristic and distinct in each species. It does not, however, always coincide with the external features used by former authors for separating the species. Through the kindness of Dr. C. H. Curran, Curator of the American Museum of Natural History, I have received a very good collection of numerous specimens which show that the wing pattern in *Tricyclea* is not as constant as was previously believed. This can be detected from specimens of the same batch, that is to say specimens collected at the same time and from the same locality, which show equal hypopygia, but a different wing pattern. Another variable feature is the chaetotaxy of the mesonotum, which I detected from a batch of *H. unicolor* Bigot reared by me from a mushroom. These specimens probably represent the offspring of a single female. The following table of fifteen males demonstrates the variability of the acrostichal and dorsocentral bristles and even an asymmetrical pattern of the *dc* which have been used for separating two groups, with 3 *dc* and with 4 *dc*, within the genus *Hemigymnochaeta* :

Hemigymnochaeta unicolor Bigot, ♂.

	dc.	*ac.*	*ac.*	*dc.*		*dc.*	*ac.*	*ac.*	*dc.*
1	3/4	3/3	3/3	3/4	9	2/3	3/3	3/3	2/4
2	2/4	3/3	3/3	2/4	10	2/4	3/3	3/3	2/4
3	2/4	3/3	3/3	2/4	11	2/4	3/3	3/3	2/4
4	2/4	3/4	3/4	2/4	12	2/4	3/3	3/3	2/4
5	2/4	3/4	3/3	2/4	13	2/4	3/3	3/4	2/4
6	2/4	3/4	3/3	2/4	14	2/4	3/3	3/3	2/4
7	2/4	3/3	3/3	2/4	15	2/4	3/3	3/3	2/4
8	2/4	3/3	3/3	2/4					

A variability in the chaetotaxy and in the colour pattern is not so surprising and has also been found to occur in other groups of the higher flies. But I have come to the conclusion that the structure of the male eyes is also not of specific value. There are evidently, in the same species, strains with the facets uniformly small and those with sharply differentiated ones, the upper facets being much bigger than the ventral ones. In one series of *H. unicolor* from Robertsport, Liberia, this feature is more or less transient, so that it is not possible to draw a sharp line between one strain and the other.

These features which occur in " specific " units with identical hypopygia probably represent strains which are not yet genetically separated, and they are therefore not to be regarded as species. But they may represent " species *in statu nascendi.*"

A further interesting point is that these strains occur independently in different species, a fact which is well known to the geneticist, and designated by Vavilov as " homologous series of mutations " (cf. Mayr, 1949, Vavilov *in* Huxley, 1949). These homologous series concern, in the genera *Hemigymnochaeta* or *Tricyclea* respectively, the wing pattern (spotted or totally hyaline), the number of the dorsocentral bristles (3 or 4 postsutural ones) and the shape of the male facets.

The problem is how to name these " strains." Many taxonomists will undoubtedly prefer to give each strain a different name, perhaps as " var." or even as " subspecies." I do not believe that this is advisable. Our taxonomic system is already sufficiently complicated by names dependent on the rules of nomenclature. In 1937 Heikertinger proposed to designate those " homologous " forms occurring in the same genus, or even in related genera, by the same term, which does not bear the name of the original author and which is not susceptible to the rules of nomenclature. The same is done by the geneticists with their " races." In the present case we should have the following designations :

(1) f. *maculata* = wings spotted.
(2) f. *immaculata* = wings totally hyaline.
(3) f. *macrommatidiata*—IV *dc* = large facets and 4 *pst dc.*
(4) f. *macrommatidiata*—III *dc* = large facets and 3 *pst dc.*
(5) f. *micrommatidiata*—IV *dc* = small facets and 4 *pst dc.*
(6) f. *micrommatidiata*—III *dc* = small facets and 3 *pst dc.*

The terms used for designating the different parts of the male hypopygium have been explained in a paper by Zumpt and Heinz (1950). The aim of that paper was to propose a set of international terms which are necessary for taxonomic purposes. The conclusions we drew were based chiefly on papers by Patton, Rohdendorf, Séguy and Hennig. Unfortunately, owing to war time conditions, we did not know of the papers by Crampton (1944) and Hardy (1944), who both came to quite different conclusions regarding the homologies of the parts of the Calliphorid terminalia. I have not yet been able to check the findings of these authors, which have chiefly an academic interest, but intend to do this in the near future, and would not be surprised if the new theory by Crampton and Hardy proves to be correct. The question is whether for practical purposes, like the identification of species, it is necessary or even advisable to create strictly homologous terms which are always liable to be changed according to the most recent advances of knowledge. Would it not be preferable to use analogous or independent terms? Those authors who wish to deal with phylogenetic problems may then explain the analogous terms for their special purposes.

The following descriptions of the different species are given in the usual manner, with details of the chaetotaxy, but it must be taken into consideration that the number and arrangement of the bristles on the thorax and the legs may be more variable than stated from the specimens on which these descriptions have been based. The deciding feature should always be, in my opinion, the hypopygium, and it should therefore be checked at least in each batch of specimens from different localities. It should be pointed out, however, that the hypopygium may also show slight variability, a fact which is sometimes overlooked by modern authors, for instance, Séguy.

The drawings have been made from microscopic slides, the hypopygia being mounted in Berlese's fluid. The hypopygia of most of the Calliphorinae are so small that it is no longer sufficient to bend them off, as is normally done in the *Sarcophaga* species. When dissected and mounted they naturally do not retain their original appearance because the coverslip flattens them to some extent, and this fact should be borne in mind when the drawings are being interpreted. However, if all genitalia are treated in the same manner they will be suitable for purposes of comparison and can be studied in more detail than is possible on the specimen, where this organ may, moreover, be shrunken or otherwise deformed.

B. KEY TO THE GENUS *Hemigymnochaeta* CORTI.

1 (14) Fifth abdominal tergite without paired apical spots which are sometimes fused forming a narrow marginal band. Wholly brown or black, or the disc more or less darkened . . . . 2.

2 (5) Mesonotum wholly orange or yellow-brown, without dark pattern . 3.

3 (4) Posterior strongly sclerotised side (harpes) of phallosome not triangularly widened terminally, paralobi club-shaped, cerci bi-tipped, not enlarged in the middle (fig. 2). Mesonotum with 3 or 4 *pst dc*, upper facets in male large or small. Wings wholly hyaline. 6–8 mm. Ethiopian region . . . . . 1. **unicolor** (Bigot)

4 (3) Posterior side of phallosome triangularly widened terminally, paralobi slender, cerci uni-tipped but widened in the middle (fig. 3). Liberia, Nigeria, Transvaal . . . . 2. **bequaerti** Curran

5 (2) Mesonotum with a more or less pronounced dark pattern . . . 6.

6 (7) Mesonotum with 3 *pst dc*, costal region of wings brown; 6–7 mm. French Congo, Nigeria . . . . 7. **roubaudi** Séguy

7 (6) Mesonotum with 4 *pst dc* . . . . 8.

8 (9) Costal region of wings brown, mesonotum with two longitudinal vittae. Eyes in male with large upper facets. 7 mm. Portuguese East Africa . . . . 6. **gracilis** (Séguy)

9 (8) Wings wholly hyaline, costal region not differently coloured . . 10.

10 (13) Mesonotum with two longitudinal vittae . . . . 11.

11 (12) Thoracic squama narrow, equally rounded. Eyes of male with large or small upper facets. Hypopygium with relatively broad, more or less parallel sided paralobi (fig. 4). 6–8 mm. S. and E. Africa . . . . 3. **varia** (Hough)

12 (11) Thoracic squama broader, more or less truncated. Eyes of male with large upper facets. Hypopygium with strikingly club-shaped paralobi (fig. 5). 7 mm. S. Rhodesia . . . . 4. **laticeps** sp. n.

13 (10) Mesonotum with a dark, more or less extended single discal spot. Eyes of male with large and small upper facets. 7–8 mm. Liberia, S. Rhodesia . . . . 5. **liberia** Curran

14 (1) Fifth abdominal tergite with paired apical spots which are sometimes fused . . . . 15.

15 (16) Mesonotum without dark pattern, wings more or less brownish tinged but without demarcated costal area. Upper facets in male small, 4 *pst dc*. 5–8 mm. . . . 8. **apicifera** Curran

16 (15) Mesonotum with the disc blackened, costal area of wing darker brown, demarcated. Upper facets in male small, 4 *pst dc* 9. **mitis** Curran

1. *Hemigymnochaeta unicolor* (Bigot).

H. unicolor seems to be distributed over the whole Ethiopian Region and represents, together with *H. varia*, the most common species of the genus. The hypopygium resembles that of *varia*, but the cerci are slightly bi-tipped and the paralobi more or less club-shaped. The mesonotum is unicolorous, whereas in *varia* it always shows a black pattern. The wings always seem to be totally hyaline. All four forms of the chaetotaxy of the mesonotum and the structure of the male eyes exist. I have seen f. *macrommatidiata*—IV *dc* from S.W. Africa, S. Rhodesia, Transvaal and Natal, f. *macrommatidiata*—III *dc* from S.W. Africa and Liberia, and f. *micrommatidiata*—III *dc* from Liberia, Belgian Congo and S. Rhodesia. The first form probably represents *H. lutea* Corti, the type of *Hemigymnochaeta*. The second does not seem to have been named before, and the third is probably identical with *Ochromyia unicolor* Bigot, *Zonochroa flaveola* Bezzi and *Hemigymnochaeta clara* Curran. I have not seen any of the holotypes of these species. I have not yet come across a f. *micrommatidiata*—IV *dc*, but suggest that it may be represented by *Tricyclea flavella* Villeneuve.

As will be seen from the key, I have not succeeded in separating *H. bequaerti* Curran from *H. unicolor* on external features. It is, therefore, not possible to identify the females of these two species. The shapes of the hypopygia are quite distinct. *H. bequaerti* seems to be less common than *unicolor*, but may occur in the same locality.

Male.—Eyes touching, frontal stripe triangular, yellow-brown, only developed in the lower half; face yellow, antennae orange. Inner vertical bristle long and strong, *oc* short and weak, *ev*, *f* and *fo* wanting, about 5 *paf*, vibrissa long, lower third of facial ridge and buccae with black hairs, peristome with a row of strong bristles, parafacialia in the upper part with a few black setae. Mouth-parts yellow, palpi slightly widened terminally.

Thorax wholly orange; $ac = 2\text{–}3 + 3\text{–}4$, $dc = 2\text{–}3 + 3\text{–}4$, $ia = 1 + 3$, $ph = 3$, $h = 3$, $prs = 1$, $n = 2$, $sa = 3$, $sc = 4\text{–}5 + 1$, $st = 1 : 1$, $pst = 1\text{–}2$, $pp = 1\text{–}2$. Pro- and post-stigma yellow. Wings hyaline, veins yellow brown, costal spine short, r_5 with setae on both sides which nearly reach *r–m*, squama narrow, equally rounded, haltere yellow. Legs yellow, fore-tibia with 4 short *ad* and one long submedian *pv*; mid-tibia with one submedian *av* and *ad* and two median *pv*; hind-tibia with 3–4 stronger *ad*, one submedian *av* and one weak submedian *pd*.

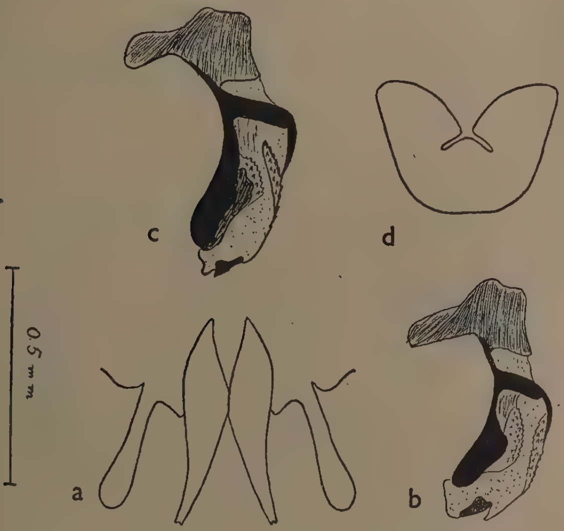

FIG. 2.—*Hemigymnochaeta unicolor* (Bigot). (*a*) Cerci and paralobi in frontal view; (*b*) and (*c*) phallosomes, to show the variability; (*d*) fifth sternite.

Abdomen mostly with a more or less distinct black pattern, rarely wholly brown, the last (5th) visible tergite never with a pair of apical spots, but ill-defined, black or dark brown. Fourth tergite normally in the terminal half and in the middle blackened; 3rd with a narrow black margin and a more or less distinct median triangular spot. This pattern, however, is considerably variable. Hypopygium (fig. 2) with the paralobi slightly variable in shape.

Female.—Width of frons at the vertex about half the length of the eye, slightly narrowed to the antennal groove. Upper part of frontal stripe and parafrontalia sometimes blackened. The chaetotaxy consists of long and well-developed *iv*, *ev*, *oc*, *f* and 1 *fo*, row of parafrontals complete. Other features as in the male.

Length.——6–8 mm.

Biology.—Cuthbertson (1935, 1939) reared this fly as (*H. clara* Curr.) from mushrooms in S. Rhodesia. I myself have reared them from a mushroom in Johannesburg.

Distribution.—Probably to be found everywhere in the Ethiopian Region. I have seen specimens from the following localities:

Liberia : Robertsport (f. *micrommatidiata* and *macrommatidiata*—III *dc*) ;

Belgian Congo : Nyashelli (f. *micrommatidiata*—III *dc*),

S.W. Africa : Grootfontein and Okakarara (f. *macrommatidiata*—III and IV *dc*), Omatjette and Epukiro (f. *macrommatidiata*—III *dc*) ;

S. Rhodesia : Salisbury (f. *macrommatidiata*—IV *dc* and *micrommatidiata*—III *dc*), Bindura (f. *micrommatidiata*—III *dc*) ;

Transvaal : Pietersburg, Naboomspruit, Barberton, Pretoria, Johannesburg, Waterval Onder (f. *macromattidiata*—IV *dc*) ;

Natal : Umbilo (f. *macrommatidiata*—IV *dc*).

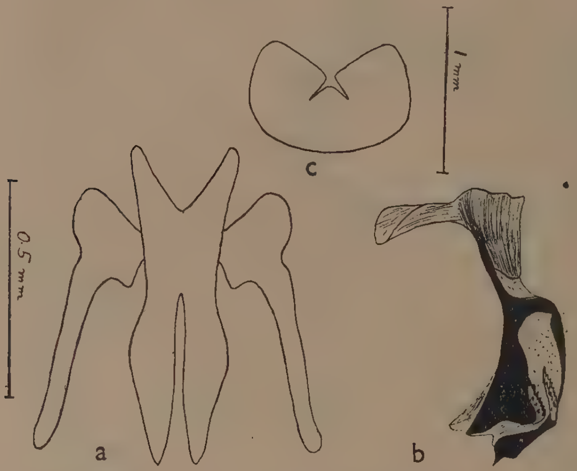

Fig. 3.—*Hemigymnochaeta bequaerti* Curran. (*a*) Cerci and paralobi in frontal view ; (*b*) phallosome ; (*c*) fifth sternite.

2. *Hemigymnochaeta bequaerti* Curran.

A second species closely related to *H. unicolor* was found amongst the material from Robertsport, Liberia, kindly submitted to me by Dr. Curran. It can only be separated from this species by the hypopygium, which is very characteristic and distinct (fig. 3) and not by the external features. This species has been described by Curran as *H. bequaerti* from Paiata, Liberia, but was based on a specimen which has an abnormally brownish-tinged costal margin. The author probably thought that this was an important feature. The specimens from Robertsport before me, however, show that there are all transitions from totally hyaline wings to those with a brownish margin. The identity between these specimens from Robertsport and the holotype has been proved by dissecting the genitalia.

In the series from Robertsport, Liberia, alone, I detected three forms corresponding to those in *H. unicolor*. These are f. *macrommatidiata*—III *dc* and IV *dc* and f. *micrommatidiata*—IV *dc*. The holotype is represented by this last form, which I have also seen from Maiduguri, Nigeria. The f. *macrommatidiata*—IV *dc* has also been reared from a mushroom collected near New Agatha, Transvaal. A forma *micrommatidiata*—III *dc* is not yet known.

3. *Hemigymnochaeta varia* (Hough).

H. varia, like *H. unicolor*, has been described several times, but up to now only two forms have been detected, namely f. *macrommatidiata*—IV *dc* and f. *micrommatidiata*—IV *dc*. Hough (1898) originally described this species as *Parachromyia varia* from Somaliland. I have not seen the type and the description does not disclose whether the author had a specimen with big or with small facets before him. Townsend (1918) created the first synonym, describing *Auchmeromyiella angola*. It has been synonymised by Malloch (1929) with *Tricyclodes pallens* Curran (1922), of which I was able to study the holo- and paratypes. These last two forms belong to f. *macrommatidiata*—IV *dc*. I further checked the type of *Tricyclodes difficilis* Curran, which is not a synonym of *H. lutea* Corti = *H. unicolor* Big. (cf. Malloch, 1929), but represents the f. *micrommatidiata*—IV *dc* of *varia*. From the specimens in Cuthbertson's collection (Salisbury) seen by Villeneuve, it is evident that *H. tridentata* Vill. (1936) is also only a f. *micrommatidiata*—IV *dc* of *varia*, with a more extended pattern on the mesonotum.

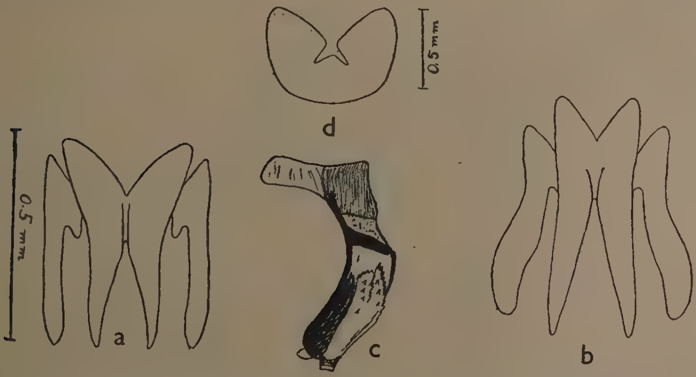

FIG. 4.—*Hemigymnochaeta varia* (Hough). (*a*) and (*b*) Cerci and paralobi in frontal view, representing slight variations; (*c*) phallosome; (*d*) fifth sternite.

Male.—Eyes touching as in *unicolor*, but the contact zone is a little shorter than in that species, *paf* mostly 6–8, 3rd antennal segment more or less darkened. Otherwise as in *unicolor*. Thorax with a dark pattern which consists of two ill-defined longitudinal stripes between the *ac* and *dc*. They end before the scutellum or are continued to it, forming there a single discal spot; *ac* = 3 + 3, *dc* = 2 + 4, *ia* = 1 + 3, *ph* = 3, *h* = 2–3, *prs* = 1, *n* = 2, *sa* = 3, *sc* = 4–5 + 1, *st* = 1 : 1, *pst* and *pp* = 1–2. Wings and legs as in *unicolor*. Abdomen with a variable pattern which can be so much extended that the last two tergites are totally black, and the third has the hind margin more or less broadly darkened. In lighter coloured specimens, the last tergite is totally or discally blackened, and the fourth and third have a broad band at the hind margins and a more or less triangular spot in the mid-line. Hypopygium (fig. 4) with the phallosome similar to that of *unicolor*, cerci pointed and paralobi relatively broad and slightly variable in this respect, but not strikingly club-shaped as in the following *H. laticeps* sp. n.

Female.—Width of frons at the vertex a little more than half the length of the eye, almost parallel. Frontal stripe mostly yellow or brown, rarely more or less darkened at the vertex. Chaetotaxy as in *unicolor*, from which it is separable by the pattern of the mesonotum.

Length.—6–8 mm.

Biology.—Cuthbertson (1935) reared this fly (identified as *pallens*) from cattle dung and fungus beds of termites. He also collected adults from ant-bear burrows.

Distribution.—*H. varia* is probably confined to the eastern and southern parts of Africa. I was able to check the male genitalia of specimens from the following localities :

S. Rhodesia : Salisbury (f. *macrommatidiata*—IV *dc*) ; Inyanga (f. *micrommatidiata*—III *dc*) ;

Transvaal : Pietersburg, Pretoria, Johannesburg (f. *macrommatidiata*—IV *dc*) ;

S.W. Africa : Omatjette (f. *macrommatidiata*—IV *dc*) ;

Natal : New Hanover (f. *micrommatidiata*—IV *dc*) ;

Cape Province : East London (f. *micrommatidiata*—IV *dc*)

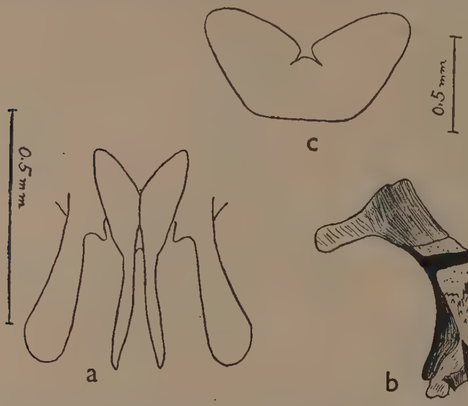

Fig. 5.—*Hemigymnochaeta laticeps* sp. n. (*a*) Cerci and paralobi in frontal view ; (*b*) phallosome ; (*c*) fifth sternite.

4. **Hemigymnochaeta laticeps** Villeneuve *in litt.*, sp. n.

In Cuthbertson's collection (Salisbury) I found three male specimens of a fairly large *Hemigymnochaeta*, which Villeneuve has seen and designated as "*laticeps* n. sp." They were collected near Gwelo and Salisbury in S. Rhodesia. A fourth male specimen has recently been collected in Salisbury by Dr. Cockbill, Entomological Division of the Agricultural Department.

This species is, with respect to the mesonotal pattern, very similar to *H. varia*, but the squama is broader in shape and is reminiscent of that of the *Tricyclea* species. The hypopygium is quite characteristic and proves it to be a good species. The cerci are relatively slender but the paralobi are distinctly club-shaped. The phallosome, however, is almost identical with that of *varia*.

Male.—Eyes touching for a long distance, the contact zone slightly longer than in *varia*, upper facets distinctly bigger than the lower ones, but transient in the median part. Face yellow to orange, chaetotaxy as in *varia* and *unicolor*.

Thorax orange with a *varia*-like pattern, scutellum with a dark disc or totally brown, $ac = 2\text{–}3 + 3$, $dc = 2 + 4$, in one specimen asymmetrically $2 + 3/4$, $ia = 1 + 3$, $ph = 3$, $h = 3$, $prs = 1$, $n = 2$, $sa = 3$, $sc = 4\text{–}5 + 1$, $st = 1 : 1$, $pst = 2\text{–}3$, $pp = 2$. Pro- and poststigma yellow. Wings hyaline, veins yellow brown, costal spine short and indistinct, r_5 with the setae almost reaching *r–m*, squama relatively broad and rounded as in *Tricyclea*, haltere yellow, legs yellow, fore-tibia with 5–6 short *ad* and one submedian long *pr*, mid-tibia with one submedian *av* and *pv* as well as with 2 median *pd*; hind-tibia with one submedian *av*, 3 longer and stronger and a row of weaker *ad* and *pd*.

Abdomen with the last tergite totally blackened, the fourth with about the hind half black and a quadrangular median spot which almost reaches the anterior margin, third and second tergites with the hind margins narrowly blackened. Hypopygium (fig. 5) with strikingly slender cerci and club-shaped paralobi.

Length.—9 mm.

Female.—Not known.

Biology.—Nothing known.

Distribution.—The description is based on 2 ♂ from S. RHODESIA: Gwelo, xi.1932 (*Cuthbertson*); one ♂ (holotype) from Salisbury, ii.1935 (*Cuthbertson*), and a further ♂ from the same locality, iv.1952 (*Cockbill*).

The material has been returned to Salisbury except one male from Gwelo which is now in the collection of the South African Institute for Medical Research, Johannesburg.

5. *Hemigymnochaeta liberia* Curran.

This species has been based by Curran on a single female from Du River, Liberia. I have found, among the material submitted to me by Dr. Curran, a specimen which undoubtedly represents the other sex of *liberia*. I dissected its genitalia, which proved to be quite characteristic and distinct from those of other *Hemigymnochaeta* species so far described. In addition I have received several males and females from S. Rhodesia *ex* Cuthbertson's collection and *ex* the American Museum of Natural History, which are, with respect to the genitalia, very similar to the Liberian specimen. The genitalia of four of the Rhodesian males, two *micrommatidiata* and two *macrommatidiata*, do not show a significant variability, but they differ from those of the typical *liberia* in having broader paralobi, a less strongly sclerotised phallosome, and they differ slightly in the shape of the 5th sternite. It is possible that the only Liberian male represents an aberration, and that the investigation of more males will prove the identity of the western and eastern forms. As this is improbable, however, I propose to distinguish the eastern form as a subspecies and to name it *H. liberia orientalis* subsp. n.

The male of *H. liberia liberia* belongs to the f. *macrommatidiata*—IV *dc*. Among the males of subsp. *orientalis* the f. *macrommatidiata*—IV *dc* as well as f. *micrommatidiata*—IV *dc* are represented.

(a) *H. liberia liberia* Curran.

Male.—Eyes touching, upper facets large and demarcated from the lower ones, frontal stripe triangular, orange, only developed in the lower half, face yellow-brown and orange, 3rd antennal segment darkened at the outer margin. Inner vertical bristles strong, *oc* only hairlike, 5–6 pairs of hairlike *paf*, no *ev*, *f* or *fo*. Parafacialia on the upper part with a few setae, buccae with black hairs, vibrissa distinct, peristome with a row of hairlike bristles, of which one near the vibrissa is strikingly stronger than the others. Mouth-parts orange, palpi slightly curved and dilated towards the tip.

Thorax with the disc and the scutellum ill-defined, darkened, remaining parts yellow and orange; $ac = 3 + 3$, $dc = 2 + 4$, $ia = 1 + 2$, $ph = 3$, $h = 3$, $prs = 1$, $n = 2$, $sa = 3$, $sc = 5 + 1$, $st = 1 : 1$, *pst* and $pp = 1$. Pro- and poststigma yellow. Wings hyaline, veins brown, costal spine wanting, r_5 dorsally with the setae half way to *r–m*, squama narrow, haltere yellow. Legs yellow, fore-tibia with *ad* less distinct, but one submedian *pv*; mid-tibia has one *av*, *ad* and two *pv*; hind-tibia with 2 *ad* and one submedian *av*, none of them very strong.

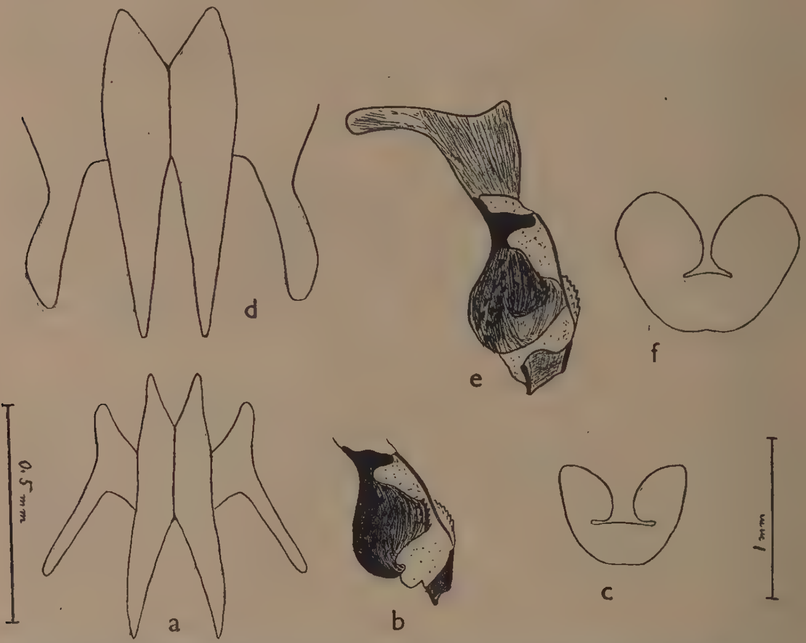

FIG. 6.—*Hemigymnochaeta liberia* Curran. (*a*) to (*c*) Cerci with paralobi, phallosome and fifth sternite of ssp. *liberia* Curran; (*d*) to (*f*) same organs of *orientalis* ssp. n.

Abdomen with the last two segments and hind half of the third segment blackened, hind margin of the 2nd tergite narrowly black. Hypopygium with slender paralobi and a strongly sclerotised phallosome (fig. 6).

Female.—Frons broadest at the vertex and here almost half as wide as the length of the eye, but distinctly narrowed towards the antennal groove; upper part of frons blackened, face yellow-orange. Chaetotaxy consists of well-developed *iv*, *ev*, *f*, *fo* and 2 pairs of divaricate *oc*, row of *paf* complete. The black pattern of thorax consists of an ill-defined dark brown discal spot, the margin of the scutellum remaining yellow. The abdomen is almost totally black-brown. There is no doubt that the dark pattern in both sexes is considerably variable. Intra-alar bristles 1 + 3, the normal number in the species of this group.

Length.—7–8 mm.

Biology.—Nothing known.

Distribution.—LIBERIA. The female holotype was collected by Bequaert near the Du River, in 1924, and the only known male was found by Snyder near Robertsport, 25th November, 1942.

(b) *H. liberia* **orientalis** subsp. n.

The specimens before me, consisting of 5 males and 8 females, belong to the formae *micrommatidiata*—IV *dc* and *macrommatidiata*—IV *dc*, but probably occur together in the same biotope. They have been taken from burrows of ant-bears and termite nests near Salisbury, S. Rhodesia, in January and February, 1935.

In general appearance, the Rhodesian subspecies is more lightly coloured and has on the average a less extended dark pattern than the West African subspecies. There is, however, considerable variation. In some specimens only a median stripe, which does not reach the dorso-central bristles, and a discal spot on the scutellum remain blackish. Abdominal pattern may also be reduced so that only the hind halves of 3rd and 4th tergites are dark, whereas the 5th is totally yellowish.

Chaetotaxy of thorax and legs does not differ markedly from that of the Liberian pair. Probably in all species of Calliphorids a slight variability in the bristle pattern is to be expected. In the *orientalis* series, *ia* mostly consists of 1–3, *ad* of legs sometimes more or less indistinct among the surrounding hairs.

Length.—6–8 mm.

Holotype returned to the American Museum of Natural History, New York; paratypes in the Museum of the Entomological Division of the Agricultural Department, Salisbury, and in the S. African Institute for Medical Research, Johannesburg.

6. *Hemigymnochaeta gracilis* Séguy.

I have not seen any specimens which can be referred to this species. The author described it as *Tricyclea* and compared it with *T. unipunctata* Curran but later (1946) he transferred it to *Hemigymnochaeta*.

Body orange, mesonotum almost wholly brown with longitudinal, ill-defined vittae. Wings with a terminal costal spot. Abdomen yellow, third tergite with a broad black-brown apical band, fourth and fifth almost totally black-brown.

Length.—7 mm.

There is only one male recorded from Vila-Pery, Portuguese East Africa.

7. *Hemigymnochaeta roubaudi* Séguy.

In 1946 Séguy described another *Hemigymnochaeta* species from Brazzaville, Belgian Congo.

This species is characterised by having 3 pairs of postsutural *dc*, a median black vitta on the mesonotum and a brown costal margin on the wings. The abdomen is banded, last tergite red with the apex brownish.

It is probable that this species is a synonym of *Tricyclea fuliginosa* Villeneuve (1936), from Oshogbo, S. Nigeria.

8. *Hemigymnochaeta apicifera* Curran.

H. apicifera is only known from Liberia, and is easily recognisable by the paired black apical spots on the last abdominal tergite. It has this feature in common with *H. mitis* Curran which, perhaps, represents only a dark form of *apicifera*. The wing of *mitis* has a distinctly darker brown costal margin and the disc of the thorax is blackened, whereas it is wholly orange in *apicifera*.

Male.—Eyes touching, only a f. *micrommatidiata* known. Frontal stripe triangular, yellow brown, only developed in the lower half; face including antennae yellow. Inner vertical bristle long and strong, *oc* shorter, but distinct, *ev*, *f* and *fo* wanting, about 6–8 *paf*, upper parafacialia with black setae, vibrissa long, lower third of facial ridge and buccae with black hairs, peristome with a row of bristles of which one near the vibrissa is much stronger than the others. Mouth-parts yellow, palpi slightly enlarged terminally.

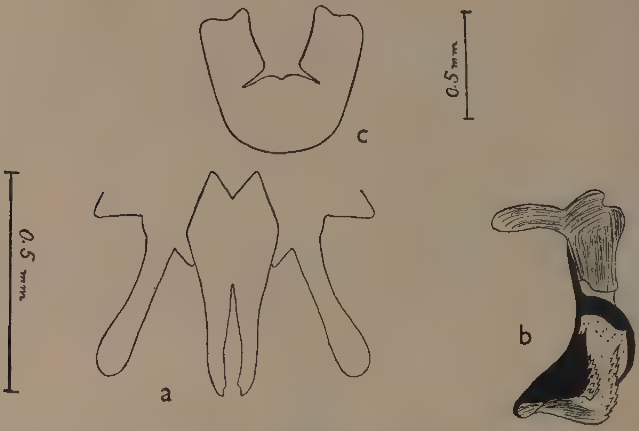

Fig. 7.—*Hemigymnochaeta apicifera* Curran. *a*) Cerci and paralobi in frontal view; (*b*) phallosome; (*c*) fifth sternite.

Thorax wholly orange, $ac = 3 + 3\text{–}4$, $dc = 2 + 4$, $ia = 1 + 2\text{–}3$, $ph = 3$, $p = 3$, $prs = 1$, $n = 2$, $sa = 3$, $sc = 5\text{–}7 + 1$, $st = 1 : 1$, *pst* and $pp = 1\text{–}3$. Pro- and poststigma yellow. Wings more or less strongly tinged and costal area in some specimens slightly demarcated, veins brown, costal spine wanting, r_5 dorsally with setae almost reaching *r–m*, squama narrow, equally rounded, haltere yellow. Legs yellow, fore-tibia with 4 or 5 stronger *ad* and one long submedian *pv*; mid-tibia with one submedian *av* and *ad* and two median *pv*, hind-tibia with two stronger *ad*, and one submedian, mostly not very strong *av* and *pd*.

Abdomen with transverse bands on the hind margins of the segments, that of the 2nd narrow, relatively broad on the 3rd and 4th and normally interrupted, forming two spots, on the 5th, no median longitudinal spots. Hypopygium (fig. 7) with cerci and paralobi similar to those of *H. unicolor*, phallosome resembles that of *H. bequaerti*.

Female.—Width of frons at the vertex almost half the length of the eye, slightly narrowed towards the antennal groove. Upper part of frontal stripe and parafrontalia more or less darkened. Chaetotaxy as in the other species of the genus.

Length.—5–8 mm.

Biology.—Nothing known.

Distribution.—Curran described this species from several males and females from Liberia: Nemeh Town, Reppo's Town and Bakra Town, viii–x. 1936. I have seen the holotype and allotype as well as numerous specimens from Bendu, near Robertsport, Liberia, ii–iv, x–xi. 1943.

9. *Hemigymnochaeta mitis* Curran.

Curran based this species on a single male from Liberia, Paiata: x. 1926. It is distinguished from *H. apicifera* by the demarcated darkened costal margin of the wing and by the blackened disc of the mesonotum and scutellum. Amongst the material from Robertsport, Liberia, I detected two female specimens, which, according to these colouring features, must be regarded as *mitis*. I did not dare to dissect the only male which is slightly shrunken and probably not very resistant to this procedure. The checking of the male genitalia must be done in the future when more material is available. It will, perhaps, only prove that *mitis* is a darker coloured form of *H. apicifera*.

C. Key to the Genus *Tricyclea* Wulp.

1 (2) Mesonotum with 3 *pst dc*. Thorax wholly yellow brown, abdomen with the posterior margins of the segments narrowly dark banded and on the 3rd and 4th tergites with a median triangular spot each. 3–4 mm. Liberia . . . . . . 1. **nana** sp. n.
2 (1) Mesonotum with 4 *pst dc* . . . . 3.
3 (18) Wings wholly hyaline, costal border not demarcated brown or with distinct spots . . . . 4.
4 (5) Mesonotum wholly orange, remaining body yellow, hind margins of abdominal segments brownish. 4 mm. French Congo 2. **ochracea** Séguy
5 (4) Mesonotum with a black pattern . . . . 6.
6 (9) Last abdominal tergite wholly reddish or brown, or with a median dark vitta, but without a pair of sharply defined apical spots . 7.
7 (8) Body reddish, mesonotum with a black dorsum, scutellum yellow, the last two abdominal tergites red-brown. 5 mm. Portuguese East Africa, S. Rhodesia? . . . . . 4. **claripennis** Séguy
8 (7) Body coloured as in the foregoing species, but abdomen with a black, variable pattern, forming more or less broad bands at the hind margins and median vittae, sometimes the last segments are totally black. 6–7 mm. Ethiopian Region 3. **semicinerea** Bezzi
9 (6) Last abdominal tergite with a pair of sharply defined, black apical spots which are sometimes more or less fused . . . . 10.
10 (11) Median black vitta between *dc* covers the whole length of the thorax including the scutellum, of which only a narrow lateral margin remains yellow. Abdomen with rather narrow black bands. Belgian Congo . . . . . 7. **resurgens** Villeneuve
11 (10) Median black vitta abbreviated posteriorly, scutellum yellow . 12.
12 (13) Male frons at the narrowest point one-fifth of eye-length. Mesonotum with the disc black, but scutellum yellow, abdominal bands narrow. 9 mm. S. Rhodesia . . . 8. **latifrons** Curran
13 (12) Male frons at the narrowest point at most one-eighth of eye length 14.

14 (17) Eyes close together, frons at the narrowest point not wider than at most twice the width of the anterior ocellus (one-twelfth of eye length) . . . . 15.

15 (16) Abdominal bands narrow, on the 3rd and 4th tergites only developed laterally, in the median line with an ill-defined, small apical spot. 5 mm. Kenya . . . . 5. **patrizii** sp. n.

16 (15) Abdominal bands broad and complete, covering $\frac{1}{4}$–$\frac{1}{2}$ of the 3rd and 4th tergites. Palpi in male as broad as the third antennal segment. 6–8 mm. West and Central Africa
6. **fasciata fasciata** (Macquart)

17 (14) Eyes more widely separated, frons at the narrowest point about one-eighth of eye length. Abdominal bands on the 3rd and 4th tergites normally not extending one-tenth of its length. 6–8 mm. South and East Africa . 6. **fasciata ferruginea** Wulp

18 (3) Wings with the costal border wholly brown, or this vitta is dissolved in two more or less distinctly separated spots . . . 19.

19 (24) Subcostal cell wholly hyaline . . . . 20.

20 (21) Thorax with the whole dorsum glossy black, only the shoulders, the post alar area and extreme tip of the scutellum remain yellow or brown. Wing with an ill-defined, dark brown costal spot which extends from the middle of the subcostal cell to the tip and forms basally a more or less distinct cloudy extension up to *r–m*. Abdominal tergites with very broad black bands which cover two-thirds or more of the 3rd and 4th segments. 7–8 mm. West and Central Africa . . . . 17. **diffusa** Malloch

21 (20) Thorax with a less extended pattern, at least the whole lateral margins of the scutellum remain yellow. Wings without a cloudy extension to *r–m* . . . . 22.

22 (23) Palpi in male distinctly narrower than the 3rd antennal segment. Wing with a single apical, costal spot which does not reach the subcostal cell. Black pattern variable, mesonotum wholly brown or with the disc more or less darkened, abdominal bands normally narrow, but sometimes broad. 6–7 mm. Liberia
9. **unipunctata** Curran

23 (22) Palpi in male as broad as the 3rd antennal segment, in female still broader. Wing with a single apical, costal spot but it reaches the subcostal cell. Mesonotum normally with a black disc. 7–8 mm. West and Central Africa . 6. **fasciata fasciata** (Macquart)

24 (19) Subcostal cell totally or partly clouded . . . . 25.

25 (38) Wing with two well separated and quite distinct costal spots . . 26.

26 (35) Third and 4th abdominal tergites with black apical bands, not totally black or black brown . . . . 27.

27 (28) Mesonotum with a pair of longitudinal black vittae which are separated from each other by the space between *ac* and which do not reach the yellow scutellum. 7 mm. Belgian Congo
10. **nigroseta** Curran

28 (27) Mesonotum with the disc more or less extended, blackened, without distinctly separated longitudinal vittae . . . . 29.

29 (30) Basal spot extending basally although often lighter coloured and less distinct beyond *sc*. Disc of mesonotum and scutellum glossy black, abdominal bands of the 3rd and 4th tergites covering one-third to one-half of the segment. 6–8 mm. Liberia
11. **similis** Curran

30 (29) Basal spot not extending beyond *sc* or not even reaching it . . 31.

31 (32) Outer posthumeral bristle lacking. Thoracic and abdominal pattern variable, the latter covering one-fifth to one-half of the segment. 4–7 mm. Kenya, Uganda, Liberia 12. **bifrons** Malloch

32 (31) Outer posthumeral bristle present . . . . 33.

33 (34) Very similar to the following species and only to be separated with certainty by the male terminalia and the fifth sternite which has a tooth-like protrusion at the inner corners formed by the median incision (cf. fig. 16). Triangular median widening of the black bands of the 3rd and 4th abdominal tergites shorter, not covering more than one-third of the segment. 6–7 mm. Nigeria, Belgian Congo . . . 13. **perpendicularis** Villeneuve

34 (33) Fifth sternite without a tooth-like protrusion at the inner corners. Triangular median widening of the black bands of the 3rd and 4th abdominal tergites larger, almost reaching the anterior margins. 6–7 mm. S. Rhodesia . . . . 14. **cockbilli** sp. n.

35 (26) Third and 4th abdominal tergites almost totally black or black brown . . . . 36.

36 (37) Mesonotum with a black disc reaching from the suture to the scutellum. 6–7 mm. Nigeria, Gold Coast 15. **semithoracica** Villeneuve

37 (36) Mesonotum with a black disc reaching from the anterior border to the roots of first *dc*, subtriangular in shape, at the posterior margin twice as wide as at the head. 6 mm. Belgian Congo 16. **currani** sp. n.

38 (25) Wing with the costal area more or less uniformly brown, the spot ill-defined; sometimes it is more or less distinctly divided by a narrow hyaline stripe near *r* . . . . 39.

39 (42) Frons of male at the narrowest point not broader than the anterior ocellus, frontal stripe therefore interrupted or at least linear . 40.

40 (41) Thorax normally with an extended pattern which covers the discs of the mesonotum and the scutellum, mesonotal disc sometimes with a lighter median area. 6–7 mm. Liberia . . 18. **du** Curran

41 (40) Thorax with two broad longitudinal vittae which do not reach the yellow scutellum. 7–8 mm. S. Rhodesia, Cape Province 19. **bivittata** Curran

42 (39) Frons of male at the narrowest point at least as broad as the ocellar triangle, frontal stripe therefore always well developed . 43.

43 (44) Mesonotum totally yellow orange. 9–10 mm. Liberia 20. **major** Curran

44 (43) Mesonotum black except for the lateral margins. 7–8 mm. Nigeria . . . . 21. **spiniceps** Malloch

1. **Tricyclea nana** sp. n.

A small species with 3 *pst dc* on the mesonotum and therefore easily separable from all the other *Tricyclea* species which have 4 *pst dc*. Wings totally hyaline.

Male.—Eyes with small facets but with a transition from the smaller ventral ones to the slightly larger upper ones. Frons at the narrowest point about as wide as the anterior ocellus (one-fifteenth of eye-length), frontal stripe yellow orange, not interrupted, but very narrow in the middle; face yellow, 3rd antennal segment sometimes a little darkened. Inner verticals and a pair of proclinate *oc* well developed, one post-orbital bristle on each side which is a little longer than the others, probably represents the *ev*; *f* and *fo* wanting, 5–6 *paf*, vibrissa long, facial ridge, parafrontalia and facialia as well as the buccae relatively densely beset with bristle hairs, peristome with a row of bristles. Mouthparts yellow, palpi slightly widened terminally and beset with spine-like bristles.

Thorax wholly orange or with a more or less distinct, dark brown, narrow median stripe, *ac* = 2–3 + 3, *dc* = 2 + 3, *ia* = 1 + 2, *ph* = 1, *h* = 3, *prs* = 1, *n* = 2, *sa* = 3, *sc* = 5 + 1, *st* = 1 : 1, *pst* and *pp* = 1. Pro- and poststigma yellow, postalar declivity bare. Wings hyaline, veins yellow, costal spine well developed, r_5 dorsally with setae up to *r–m*, squama narrow, as in *Hemigymnochaeta*, haltere yellow. Legs yellow, fore-tibia with 2 *ad* and one submedian *pv* ; mid-tibia with one submedian *av* and two *ad* and *pv* ; hind-tibia with two *ad*, and one submedian *av* and *pd*.

Abdomen yellow-brown, hind margins of the 2nd–4th tergites narrowly blackened, and on the 3rd and 4th with a more or less distinct narrow, triangular spot, last tergite without pattern. Hypopygium (fig. 8) with slender cerci and paralobi.

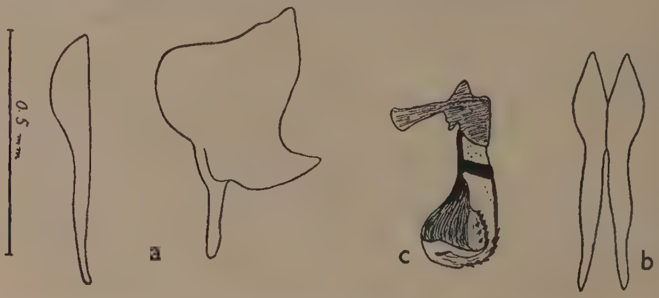

Fig. 8.—*Tricyclea nana* sp. n. (*a*) Cerci and paralobi in lateral view ; (*b*) cerci in frontal view ; (*c*) phallosome.

Female.—Frons very broad, at the vertex almost three-quarters of eye length, widened towards the antennal groove, totally yellow brown. Chaetotaxy of head complete, with *ev*, *iv*, *oc*, *f* and two *fo*.

Length.—3–4 mm.

Biology.—Nothing known.

Distribution.—The description is based on 3 males and 3 females from Liberia : Bendu, Robertsport, iii, iv, x–xii.1942/43 (*Snyder*). Holotype (♂) and 3 paratypes (1 ♂, 2 ♀) returned to the American Museum of Natural History, New York, one pair retained for the collection of the South African Institute for Medical Research, Johannesburg.

2. *Tricyclea ochracea* Séguy.

I have only seen one female specimen from S. Rhodesia : Balla-Balla, iii.1931 (*Cuthbertson*) which may be referable to this species.

The species was described from a male specimen from Ogooué, French Congo. According to the description, the male eyes have enlarged upper facets and are touching. Antennae yellow-orange, the third joint two and a half times as long as the second. Thorax yellow with the mesonotal disc red-orange, 4 *pst dc*, femora and tibiae yellow, tarsi brownish. Abdomen yellow, hind margins of tergites ill-defined, brownish.

Length.—4 mm.

3. *Tricyclea semicinerea* Bezzi.

Bezzi (1908) based this species on a female specimen from Eritrea. In 1927, Curran described a *T. palliventris* from South Africa which Malloch (1929) suggested might be synonymous with Bezzi's species, an opinion which I endorse. Furthermore I also believe that Malloch's *T. analis* Malloch (1929) is only a *T. semicinerea.* The presence or absence of an outer posthumeral bristle is hardly of specific value, but the types have yet to be checked. *T. analis* was described from Angola.

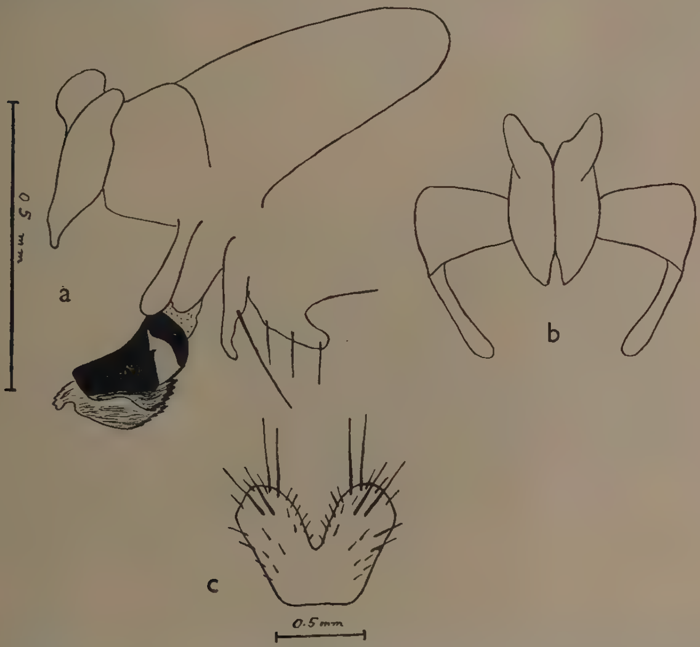

FIG. 9.—*Tricyclea semicinerea* Bezzi. (*a*) Hypopygium in lateral view; (*b*) cerci and paralobi in frontal view; (*c*) fifth sternite.

T. semicinerea has a relatively extended but variable black pattern on the thorax and abdomen. This pattern, 4 *pst dc*, unspotted wings and the absence of apical spots on the last abdominal tergite, distinguish *T. semicinerea* from the bulk of the *Tricyclea* species. Hypopygium very characteristically shaped.

Male.—Eyes with small facets, frons very narrow, at the narrowest part not wider than the anterior ocellus, frontal stripe yellow, linear between the eyes, face yellow, silvery tomented and with black setae, *iv* and proclinate *oc* developed, about 6 *paf*, vibrissa long and thick, lower half of facial ridge and buccae with black hairs. Mouth-parts yellow, palpi only slightly widened towards the tip.

Thorax always with an extended black pattern which may be restricted to the mesonotal disc between the *ia* and the scutellum, or it may cover also the sides of the mesonotum and the base of the scutellum and even the pleurae, whereas the tip always remains yellow. Chaetotaxy; *ac* = 3 + 3, *dc* = 2 + 4, *ia* = 1 + 3, *ph* = 2–3, *h* = 3, *prs* = 1, *n* = 2, *sa* = 3, *sc* = 5 + 1, *st* = 1 : 1, *pst* and *pp* = 1–2. Pro- and poststigma yellow. Postalar declivity with a few fine hairs. Wings hyaline, veins brown, costal spine distinct, r_5 with a row of setae which ventrally pass, and dorsally almost reach *r–m*, squama broad, haltere yellow. Legs yellow, hind-femur sometimes more or less blackened, fore-tibia normally with 3 relatively short *ad* and one long submedian *pv*, mid-tibia with one submedian *ad* and *av*, 2 *pv*; hind-tibia with 2 *ad*, *av* and *pd*.

Abdomen with an extended but variable black pattern, hind tergite normally wholly black or dark brown, fourth tergite black for the greater part, the lateral corners more or less brown, hind margins of the 2nd and 3rd tergites blackened and the median part of the third tergite with a black vitta, which varies in size but normally reaches the front margin. Hypopygium (fig. 9) very strikingly shaped with short and broad cerci, slender paralobi and a stout phallosome, 5th sternite of primitive shape.

Female.—Frons at vertex about two-thirds of eye length, slightly widened towards the antennal groove, parafrontalia and facialia with a silvery dusting as in the male, but broader, *iv*, *ev*, *f* and 1 *fo* present.

Length.—6–7 mm.

Biology.—Nothing known.

Distribution.—*T. semicinerea* probably occurs all over the Ethiopian Region. I have seen specimens from LIBERIA: Robertsport; N. RHODESIA: Chingola; SOUTHERN RHODESIA: Salisbury, Gatooma, Filabusi, Balla-Balla; TRANSVAAL: Pretoria, Barberton.

4. *Tricyclea claripennis* Séguy.

Séguy based this species on a single male from the Zambesi river near Chemba, Portuguese East Africa. I have before me a single female from Gatooma, S. Rhodesia, which I refer doubtfully to this species. *T. claripennis* Séguy differs from *T. semicinerea* Bezzi in that the abdomen has no black pattern, and the last two segments are, according to Séguy's description, red-brown instead of yellow-brown like the remaining anterior segments. In the above-mentioned female, only the last segment is a little darker brown.

5. **Tricyclea patrizii** sp. n.

Only one male is known of this species which is well characterised by its hypopygium. It was sent to me by the Commonwealth Institute of Entomology, who received it from Dr. S. Patrizi.

Male.—Eyes with the upper facets slightly larger than the ventral ones, and with transitional forms between the two; frons, at the narrowest part, almost twice as wide as the anterior ocellus (one-twelfth of eye length), frons and face yellow-orange, frontal stripe complete, parafrontalia and facialia with a slight silvery dusting and beset with black setae; *iv* and *oc* are broken off in the specimen before me, but, judging from the traces they must be well developed; one longer post-orbital bristle on each side probably represents the *ev*; *f* and *fo* wanting, 4 long and 2 short *paf*, vibrissa long and thick, lower half of facial ridge, peristome and buccae with black bristles; mouth-parts yellow, palpi slightly widened towards the tip.

Thorax yellow-brown with a black disc which covers the space between the inner *ph* and *ia* and ends just before the scutellum which remains yellow; *ac* = 3 + 3, *dc* = 2 + 4, *ia* = 1 + 3, *ph* = 3, *h* = 3, *prs* = 1, *n* = 2, *sa* = 3, *sc* = 4 + 1, *st* = 1 : 1, one strong and several weaker *pst* and one strong and one weak *pp*. Pro- and poststigma yellow, postalar declivity with a few black setae. Wings hyaline, veins yellow-brown, costal spine wanting, r_5 with fairly long setae which surpass *r–m* for a long distance ventrally, and only for a very short distance dorsally. Squama broad, haltere yellow. Legs yellow, fore-tibia with 4 relatively short *ad* and one submedian *pv*; mid-tibia with one submedian *a* and two *p*; hind-tibia with 2 *ad* and one submedian *ad*.

Abdomen yellow-brown, hind margins of 3rd and 4th tergites with very narrow black bands which are only developed laterally and disappear in the median part; 3rd and 4th tergites each bear a small, ill-defined, median apical spot, 5th tergite has paired apical spots. Hypopygium of very outstanding shape (fig. 10), the cerci are broad and united for almost the whole length, forming a structure like a shovel; phallosome of normal shape.

Length.—5 mm.

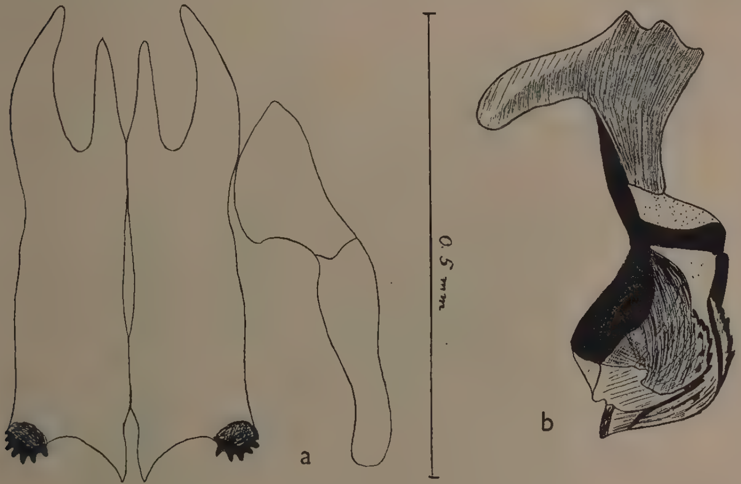

FIG. 10.—*Tricyclea patrizii* sp. n. (*a*) Cerci and paralobi in frontal view; (*b*) phallosome.

Distribution.—The only male was reared by Dr. S. Patrizi from a pupa found in a termite nest, KENYA: Nairobi, v.1945. British Museum (Natural History).

6. *Tricyclea fasciata* (Macquart).

This is the earliest described species of this genus on which Brauer and Bergenstamm founded their genus *Zonochroa*. The type species of *Tricyclea*, however, is *ferruginea* Wulp, regarded in this paper as the oriental subspecies of *fasciata*.

T. fasciata is a relatively large species with an extended black pattern in the western subspecies and a more or less reduced one in the eastern form. The typical form includes two strains, one with spotted wings, which may be designated a *f. maculata* (= *fasciata* Mcq., *exarsa* B.B.), and a f. *immaculata* in which the wings are wholly hyaline (= *evanida* Villen., *kasatana* Curr.). *T. fasciata ferruginea* is only known in the immaculate form. The shape of the hypopygium is exactly the same in both subspecies.

(a) *T. fasciata fasciata* (Macquart).

Male.—Eyes almost touching, upper facets a little longer than the ventral ones but with transitional forms between the two kinds; frons line-shaped, narrower than the anterior ocellus, frontal stripe yellow like the face, triangular, only developed in the lower half; *iv* long and thick, *ev* only a little longer than the postorbitals, *oc* proclinate, distinct, but not very long, *f* and *fo* wanting, normally 6–8 *paf*, setae on the parafrontalia and parafacialia very scarce and indistinct, almost wanting, buccae with predominating black hairs, a few light coloured ones in the posterior part only. Vibrissa long and strong, facialia with black bristles in the lower half, peristome with a row of long bristles. Mouthparts yellow, palpi spoon-like, dilated towards the tip, but not as strongly as in the female sex.

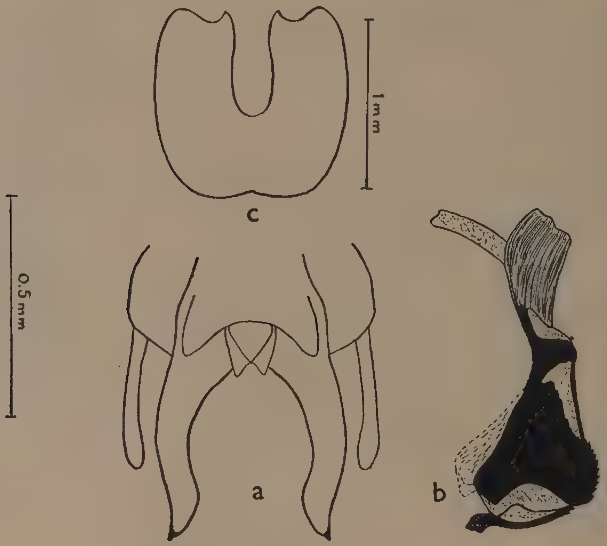

FIG. 11.—*Tricyclea fasciata* Macquart. (*a*) Cerci and paralobi in frontal view; (*b*) phallosome; (*c*) fifth sternite.

Thorax with a discal spot which normally extends between the inner *ph*, the *ia* and the base of the scutellum. The disc of the scutellum and partly the pleurae, are sometimes more or less darkened. In the f. *immaculata*, the black pattern may also be reduced, so that only the median part between the *dc* remains black; $ac = 3 + 3$, $dc = 2 + 4$, $ia = 1 + 3$, $ph = 3$, $h = 3$, $prs = 1$, $n = 2$, $sa = 3$, $sc = 6 + 1$, $st = 1:1$, *pst* and $pp = 1$–2. Pro- and poststigma yellow. Wings more or less brownish tinged and with a dark, marginal spot which covers the costal area between the tip or r_1 and r_{2-3} or r_{4-5} respectively, or, the wings may be totally hyaline. Costal spine wanting, r_5 with setae on both sides which do not pass *r–m*; postalar declivity with a few odd hairs, squama broad, haltere yellow. Legs yellow, tip of hind femur usually with a dark dorsal spot. Foretibia normally with 3 *ad* and one submedian *pv*; mid-tibia with one submedian *av*, *ad* and two *p*; hind-tibia with 2 *ad* and *pd*.

Abdomen yellow brown, 3rd and 4th tergites with relatively broad, black marginal bands which normally cover a quarter to a half of the segmental length. These bands are a little widened in the median line but do not form isolated triangular spots. The last segment bears paired apical spots which are sometimes fused. Hypopygium (fig. 11) with strong cerci, but relatively weak paralobi.

Female.—Frons at vertex almost one-third of eye length, very slightly widened towards the antennal groove, upper part of frons not blackened, but orange-yellow like the remaining part of the face. Chaetotaxy complete, *iv*, *ev*, *oc*, *f* and 1 *fo*. Palpi more strongly dilated than in the male.

Length.—6–8 mm.

Biology.—Nothing known.

Distribution.—WEST and CENTRAL AFRICA. Villeneuve records his *evanida* from the Gold Coast, Nigeria and Uganda and Malloch records it from Angola. I have seen specimens from LIBERIA: Robertsport, Zu, Paiata, Kasata; KENYA: Nairobi; and TANGANYIKA: Kilosa.

(b) *T. fasciata ferruginea* Wulp.

This subspecies looks quite different from the typical *fasciata*, but, with the exception of the width of the frons, all the separating features concern only the mesonotal and abdominal patterns.

The male frons measures about one-eighth of the eye-length, so that the frontal stripe is present up to the ocellar triangle. There are no pronounced differences in the width of the female frons in the two subspecies. The pattern is reduced, consisting of a median stripe between the *ac* or at most the *dc* on the mesonotum, and very narrow transverse bands on the abdomen which normally are not broader than one-tenth of the length of the segment. On the 3rd and 4th tergites these bands are slightly widened triangularly in the mid-line. In some specimens the marginal bands disappear totally in the median part, so that the pattern consists only of a pair of narrow lateral bands and a small, triangular median spot.

Length.—6–8 mm.

Biology.—Cuthbertson (1935) observed adults feeding on broken down fungus bed and young termite workers, and also at the honey dew of aphids.

Distribution.—This species has been described from EAST AFRICA. I have seen specimens from S. RHODESIA: Salisbury, Balla; and SOUTH-WEST AFRICA: Okakatora.

7. *Tricyclea resurgens* Villeneuve.

This species is unknown to me. The author based the description on three females from the BELGIAN CONGO and compares them with his *T. evanida* which is a synonym of the *T. fasciata* Mcq. with spotless wings (f. *immaculata*). As the females very often show a more extended dark pattern than the males, it is quite possible that *T. resurgens* has been based only on an extremely darkly coloured *fasciata*.

8. *Tricyclea latifrons* Curran.

This species can easily be separated from other *Tricyclea* species with immaculate wings and paired apical spots on the abdomen, by a relatively broad frons in the male sex which measures, at the narrowest point, one-fifteenth of the eye length. The hypopygium is quite characteristic. The nearest relatives, with respect to this organ, are *T. unipunctata* Curran, and *T. bivittata* Curran. The female sex of *T. latifrons* is not known.

Male.—Eyes with small facets, frons very broad, at the narrowest part one-fifth of eye length, frontal stripe almost parallel, yellow, parafrontalia and facialia with a slight silvery dusting, ground colour yellow like that of antennae and face, *iv* and proclinate *oc* long and strong, *ev* weak, about twice as long as the postorbital hairs, *f* and *fo* wanting, 6–7 *paf*, vibrissa long and thick, facial ridge and peristome with black bristles, buccae anteriorly with black hairs, posteriorly with yellow ones. Mouth-parts orange, palpi only slightly widened towards the tip.

Thorax with yellow-brown ground colour, but the pleura ill-defined, partly darkened, and the mesonotal disc black between the inner *ph* and the *ia*, extending to the base of the scutellum. In one of the two males before me, the discal spot is complete, in the other (holotype), it is divided into two broad, ill-defined longitudinal stripes between the *ia* and *ac*. $ac = 3 + 3$, $dc = 2 + 4$, $ia = 1 + 3$, $ph = 3$, $h = 3$, $prs = 1$, $n = 2$, $sa = 3$, $sc = 5–6 + 1$, $st = 1 : 1$, one strong and one weak *pst* and *pp* each. Pro- and poststigma yellow, postalar declivity with a few thin, lightly coloured hairs. Wings hyaline, veins yellow-brown, costal spine wanting, r_5 with a few setae which dorsally almost reach *r–m*, squama broad, haltere yellow. Legs yellow brown, hind-femur dorsally with a dark brown apical spot; fore-tibia with four *ad* and one submedian *pv*, mid-tibia with one submedian *ad* and *av*, 2 *pv*; hind-tibia with a row of *ad*, of which three are longer than the others, and two longer *pd*.

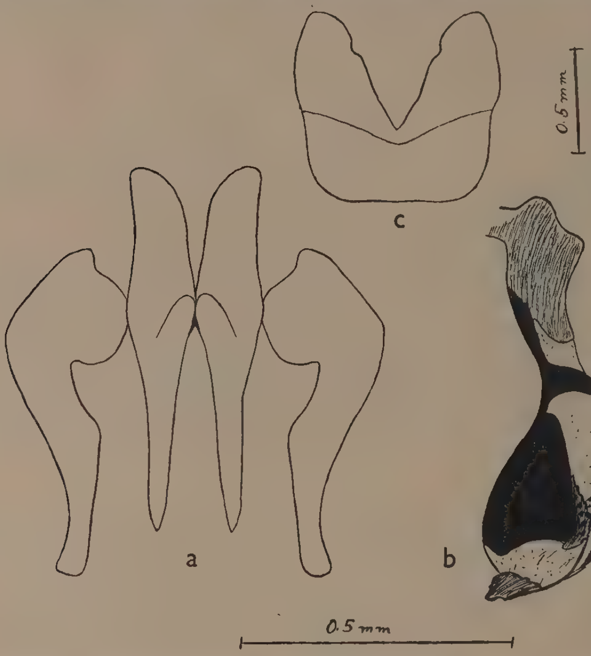

FIG. 12.—*Tricyclea latifrons* Curran. (*a*) Cerci and paralobi in frontal view; (*b*) phallosome; (*c*) fifth sternite.

Abdomen yellow-brown, third and fourth tergites with a narrow but complete marginal band which is more or less triangularly widened in the middle, fifth tergite with paired apical spots. Hypopygium (fig. 12) with slender cerci and paralobi, the latter terminally fist-shaped.

Length.—7 mm.

Distribution.—Both specimens were collected in S. RHODESIA: Salisbury, iii.1923 and ix.1936.

9. *Tricyclea unipunctata* Curran.

T. unipunctata seems to be very variable in its dark pattern. Amongst the nine male specimens before me, there are some with the whole mesonotal disc blackened, whereas in others the thorax is uniformly yellow. A similar wide variability is true for the abdominal bands which range from one-sixth to one-half of the segmental length. The costal spot is present in all specimens, in contrast to the condition in *T. fasciata*, it does not reach the subcostal cell.

Zonochroa pterostigma Bezzi is perhaps a synonym of *T. unipunctata*, as has already been pointed out by Malloch (1929). *T. liberia* Curran (1931), of which I received the type, proved to be identical with *T. unipunctata*. I also suggest that *T. gracilis* Séguy (1933) may be a mere synonym of this species. Bezzi described his species from the Gold Coast, Séguy his from the Zambesi district in Portuguese East Africa.

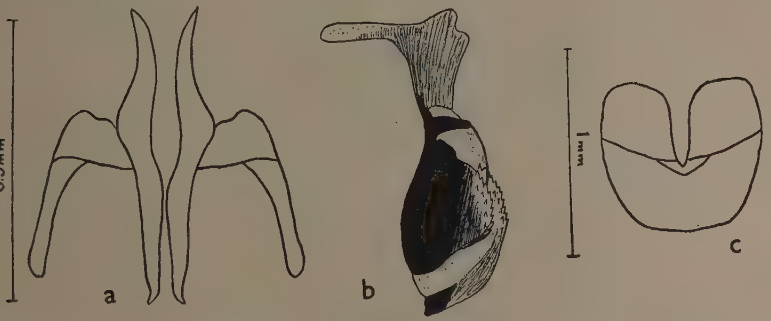

FIG. 13.—*Tricyclea unipunctata* Curran. (*a*) Cerci and paralobi in frontal view; (*b*) phallosome; (*c*) fifth sternite.

Male.—Eyes almost touching, frons line-shaped, not broader than the anterior ocellus, frontal stripe triangular, only developed in the lower part, yellow in colour like the remaining part of the face; *iv* long and thick, *ev* short, hardly longer than the postorbital bristles, *oc* proclinate, short, *f* and *fo* wanting, about 6 *paf*, parafrontalia and upper half of parafacialia with a row of short black setae, buccae with black hairs, lower half of facialia and peristome with the usual bristles. Mouthparts more or less reddish-brown, palpi of normal shape, slender and slightly dilated terminally, not spoon-shaped as in *T. fasciata*.

Thorax with a black pattern that includes the whole mesonotal disc between the inner *ph* and the *ia*, or it is totally yellow-brown. All transitions exist between these two extreme patterns. Chaetotaxy: $ac = 3 +$, $dc = 2 + 4$, $ia = 1 + 3$, $ph = 2\text{–}3$, $h = 3$, $prs = 1$, $n = 2$, $sa = 3$, $sc = 6 + 1$, $st = 1 : 1$, *pst* and $pp = 1\text{–}2$. Pro- and poststigma yellow. Wings with a terminal costal spot which does not reach the subcostal cell and the tip of the wing; remaining costal area more darkly tinged than the hind part of the wing but not distinctly spotted; costal spine wanting or at least very indistinct, r_5 with setae not surpassing *r–m*, alar declivity with a few black setae; squama broad, haltere yellow. Legs yellow brown, fore-tibia with indistinct *ad* and a long submedian *pv*; mid-tibia with one *av*, *ad* and two *pv*; hind-tibia with 2 *ad* and one submedian *av*.

Abdomen yellow brown, transverse marginal bands varying from one-sixth to one-half of the length of the segment; no triangular spot is formed in the median line. Last tergite with paired apical spots. Hypopygium (fig. 13) bears a slight similarity to that of *T. fasciata* but, nevertheless, is quite distinct.

Female.—The female sex has not yet been described, and I have no female specimens, before me.

Length.—5–7 mm.

Biology.—Nothing known.

Distribution.—The species is based on a single male from BELGIAN CONGO: Faradje. The other specimens before me were collected in LIBERIA: Zu, Robertsport, Reppo-town. Bezzi's *pterostigma* is recorded from the Gold Coast, so that the species is probably distributed over West and Central Africa.

10. *Tricyclea nigroseta* Curran.

T. nigroseta was based on a single female from Medje, Belgian Congo. I have not seen this specimen, but have another specimen before me from Faradje, Belgian Congo, which fits Curran's description. It has two spots in the costal area of the wing, the one covers the whole subcostal cell, the other lies terminally and is separated from the basal one by a light space, which has almost the same length as the basal spot. The mesonotum shows two longitudinal black vittae separated by the pale space between the acrostichal rows. Exteriorly they reach the *ia* and posteriorly they end just in front of the scutellum which remains yellow. Frons, at the vertex, has a width almost two and one-half times the length of the eye. It is distinctly widened towards the antennal groove, with *iv*, *ev*, *oc*, *f* and one *fo*, 9 *paf*. Palpi distinctly dilated terminally.

Length.—7 mm.

Nothing can be said about the validity of this species until the male sex is known.

11. *Tricyclea similis* Curran.

Similar to *T. du*, but the costal spots are distinctly separated from each other. The light space, however, is sometimes not very broad, measuring about one-fourth to more than half the length of the subcostal cell. The hypopygium is very characteristic, having strikingly short and thin paralobi.

Male.—Eyes with larger inner facets which are transitional to the smaller ventral ones; frons very narrow in the middle, linear, or eyes touching; upper frons including ocellar triangle dark brown, triangular in the lower part and yellow like in the face; *iv* well developed, *ev* wanting or indistinct, *oc* short, 5–6 *paf*; parafrontalia and upper parafacialia with a row of black setae; lower half of facial ridge, peristome and buccae with the usual black hairs or bristles respectively; mouth-parts yellow, palpi slightly enlarged terminally.

Thorax with a black pattern that covers the whole dorsum leaving only the shoulders, the extreme lateral margin of the mesonotum and of the scutellum yellow. The sterno- and hypo-pleura are sometimes almost black and large parts of the meso- and pteropleura darkened, or the pleura are totally yellow-orange. Chaetotaxy; $ac = 3 + 3$, $dc = 2 + 4$, $ia = 1 + 3$, $ph = 2$–3, $h = 3$, $prs = 1$, $n = 2$, $sa = 3$, $sc = 6 + 1$, $st = 1:1$, *pst* and $pp = 1$–2. Pro- and poststigma yellow, postalar declivity with black hairs. Wing with two long costal spots, the basal one covering the whole subcostal cell, sometimes extending basally, more or less distinctly half way to *h*; remaining part of wing brownish tinged. The second spot covers the apical half of r_{2+3}; veins dark brown, r_5 with dorsal setae up to *r–m*, costal spine very short and indistinct; squama dark brown, broad; haltere yellow. Legs yellow brown, apices of second and third femora, the hind-tibia and all tarsi more or less darkened, fore-tibia with 2–3 short *ad* and one long submedian *pv*; mid-tibia with one *av*, *ad* and two *pv*; hind-tibia with 2–3 longer *ad* and one submedian *av*.

Abdomen yellow, the second tergite with a pair of narrow marginal lateral spots; hind margins of third and fourth tergites with broad bands which cover one-third to one-half of the segment, but which do not form median spots; last tergite with paired apical spots. Hypopygium (fig. 14) similar to that of *T. bifrons* Mall., but paralobi shorter and more slender, and phallosome slightly different, fifth sternite of quite different shape.

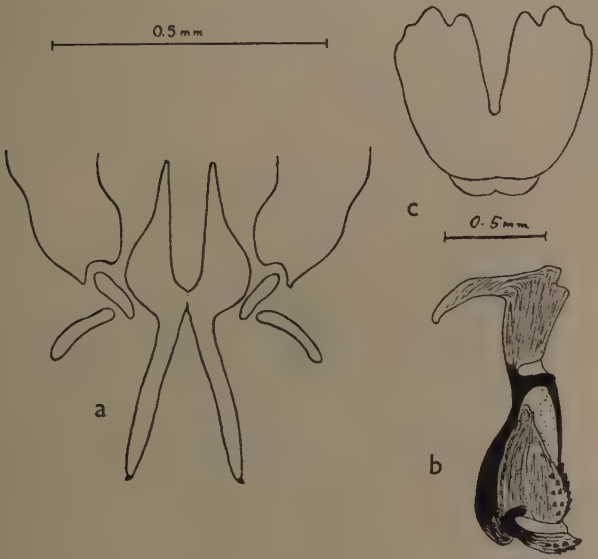

FIG. 14.—*Tricyclea similis* Curran. (*a*) Cerci and paralobi in frontal view; (*b*) phallosome; (*c*) fifth sternite.

Female.—Eyes with the upper facets smaller than in the male, but still larger than the ventral ones. Frons at the vertex about one-third of the eye length, slightly narrowed towards the antennal groove, upper half of the parafrontalia and ocellar triangle black, remaining part of frons and the face yellow and orange. Chaetotaxy complete, *iv* and *ev* long and thick, *oc*, *f* and one *fo* developed. Palpi broader than in the male sex, but not attaining width of antenna.

Length.—6–8 mm.

Biology.—Nothing known.

Distribution.—*T. similis* is only recorded from LIBERIA. I have seen specimens from Lenga Town, Reppo's Town, Zu and Bendu near Robertsport, ix.1926, vii.1928, iii, iv, xii.1943.

12. *Tricyclea bifrons* Malloch.

This species has been described twice by the author in the same paper (Malloch, 1929), as *bifrons* and as *binotata*, the differences being based on the colouring and the length of the body. These differences are, indeed, so striking that the author can hardly be blamed for his taxonomic opinion. Fortunately, I received a series of specimens belonging to this species from the Commonwealth Institute, London, which was collected in Nairobi, the typical locality of both forms, by Dr. S. Patrizi. This series includes both Malloch's species and the checking of the male terminalia reveals that both are conspecific with each other and also with a few specimens from Liberia, in the American Museum of Natural History, New York. It is possible that *T. verticella* Villeneuve (1922) is also identical with this species.

Male.—Eyes with the upper facets larger than the ventral ones, and with transitional forms between the two, frons very narrow, linear, not broader than the anterior ocellus, upper part of frons normally black, the lower half, as well as the face, yellow; third antennal segment about three times as long as the second, chaetotaxy as in *similis*, mouth-parts yellow, palpi narrow.

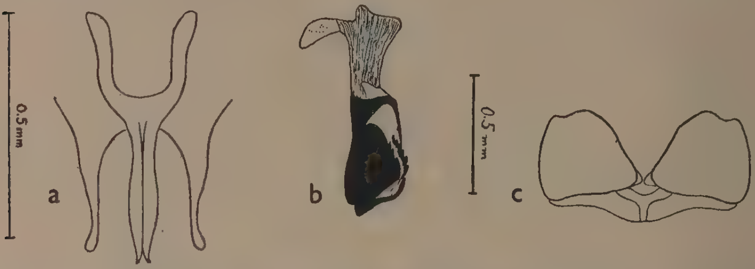

Fig. 15.—*Tricyclea bifrons* Malloch. (*a*) Cerci and paralobi in frontal view; (*b*) phallosome; (*c*) fifth sternite.

Thorax with a variable pattern, which normally covers, as in *similis*, the whole dorsum, leaving only the shoulders, the extreme lateral margin of the mesonotum and the scutellum yellow. This pattern can be considerably reduced in the following ways; the discal spots may be dissolved into two, more or less well separated, longitudinal vittae, or, the discal spots may remain entire, but be shortened in front or behind the suture; the pleura may be lightened so as to remain wholly yellow. Chaetotaxy; $ac = 3 + 3$, $dc = 2 + 4$, $ia = 1 + 3$, $ph = 2$ (outer wanting, constant ?), $h = 3$, $prs = 1$, $n = 2$, $sa = 3$, $sc = 5\text{–}6 + 1$, $st = 1 : 1$, *pst* and $pp = 1\text{–}2$. Pro- and poststigma yellow, postalar declivity with a few black setae. Wings with two costal spots as in *similis*, but the basal one shorter and not extending beyond *sc*; sometimes not even reaching it. Legs coloured as in *similis* or totally yellow-brown, chaetotaxy also as in this species.

Abdomen with a pattern as in *similis*, but the width of the bands is variable, being, in light coloured specimens, only one-fifth of the length of the segment. Hypopygium (fig. 15) with fist-tipped paralobi and a narrow fifth sternite which is almost divided.

Female.—To be separated from *similis* only by the smaller basal spot of the wing.

Length.—4–7 mm.

Biology.—Nothing known.

Distribution.—Described from Kenya: Nairobi, from which locality I have two males and two females before me. Furthermore, one male from Uganda: Kampala, and five males and females from Liberia: Bendu, Robertsport.

13. *Tricyclea perpendicularis* Villeneuve.

Villeneuve (1922) based this species on two female specimens from S. NIGERIA, and Curran (1922) described the male as *distigma* from the BELGIAN CONGO. The hypopygium is highly characteristic and shows no similarity to that of *T. bifrons*, whereas the external features of both species are very similar. *T. cockbilli* sp. n., a closely related species, which has a similar hypopygium, probably replaces *T. perpendicularis* in S. Africa.

Male.—Eyes with the upper facets only very little larger than the ventral ones; frons at the narrowest point up to twice as broad as the anterior ocellus; frons totally yellow or orange; frontal stripe linear in the middle, triangular below; face yellow; antennae orange; the third segment about three times as long as the second, *iv* and proclinate *oc* well-developed, *ev* quite indistinct, *f* and *fo* wanting, 5–8 *paf*, setae of parafrontalia and facialia wanting, vibrissa long and thick; lower third of facial ridge, peristome and anterior part of buccae with black hairs or bristles respectively; the latter measure about one-third of the eye-length; posterior part of buccae with yellow hairs. Mouth-parts yellow, palpi terminally dilated, but slightly narrower than the antennae.

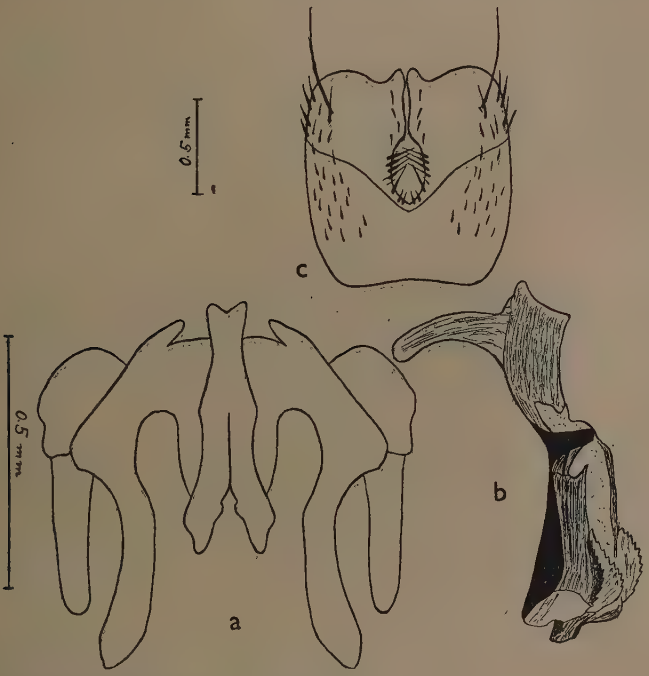

FIG. 16.—*Tricyclea perpendicularis* Villeneuve. (*a*) Cerci and paralobi in frontal view; (*b*) phallosome; (*c*) fifth sternite.

Thorax with an ill-defined, black, discal spot which may cover almost the whole dorsum including the base of the scutellum, or, it may be more or less reduced, being confined to an area between the *dc*. Chaetotaxy as in *bifrons* but the outer *ph* is present in all specimens before me and, perhaps, a constant feature. Alar declivity with fine yellow hairs.

Wings yellow; tip of hind-tibia more or less darkened; front-tibia with 3–4 *ad* and one submedian *pv*; mid-tibia with one *av*, *ad* and 2–3 *pv*; hind-tibia with several *ad* and *pd* and one submedian *av*.

Abdomen yellow, second segment without pattern, third with a narrow marginal band which is triangularly widened in the middle; fourth with a broader band which covers one-fourth to one-third of the segment; 5th with paired apical spots. Hypopygium (fig. 16) with relatively long cerci which have a finger-like, divided median lobe; fifth sternite very large, with a club-shaped incision.

Female.—I have no female specimens before me and Villeneuve's description is so short that it is not possible to give any characteristic features.

Length.—6–7 mm.

Biology.—Villeneuve mentioned that the females drop their eggs into and between the funnel-shaped openings of temporary nests of driver ants.

Distribution.—*T. perpendicularis* has been described from S. Nigeria, *T. distigma* from Boma and Faradje, Belgian Congo. I have seen specimens from NIGERIA: Maiduguri (*Snyder*), viii.1942, and from NIGERIA: Florin (*Macfie*), vii.1912.

14. **Tricyclea cockbilli** sp. n.

This species is doubtless closely related to *T. perpendicularis*, and both represent allopatric species, having evolved from former subspecies of one polytypic unit. The external features are very similar in both species but the male genitalia have already become so different that I prefer to regard them as specifically distinct and not as subspecies.

Male.—The only external differences in five males before me concern the abdominal pattern in which the median, triangular spots of the third and fourth tergites are larger and almost reach the anterior margins. More material will, however, have to be examined in order to determine whether this feature is of sufficient taxonomic value to be used for the separation of the two species. The only reliable feature is probably the hypopygium (fig. 17) which is similar to that of *T. perpendicularis*, but nevertheless quite distinct with respect to the club-shaped cerci, the shape of the median lobe, the longer paralobi and the fifth sternite.

Female.—There are three female specimens before me which probably, like the males, show a close similarity to *perpendicularis*, the female sex of which remains unknown to me. Frons at vertex a little less than one-third of the eye-length, yellow-brown, almost parallel to the antennal groove; *iv* and *ev* strong, *oc*, *f* and one *fo* present, 6–7 *paf*, parafrontalia and facialia with fine setae which are normally lacking in the male; palpi spoon-shaped, a little broader than the antennae.

Length.—6–7 mm.

Biology.—Nothing known.

Distribution.—S. RHODESIA: Salisbury, iv–viii, 4 ♂ (including holotype), 3 ♀; Melsetter district, 1 ♂. Holotype and paratypes in the Entomological Division, Agricultural Department, Salisbury; further paratypes in the American Museum of Natural History, New York, and in the South African Institute for Medical Research, Johannesburg.

The species is named in honour of Dr. G. F. Cockbill, curator of the Entomological Division, Agricultural Department, Salisbury.

15. *Tricyclea semithoracica* Villeneuve.

This species has remained unknown to me and I believe it possible that it may represent an extreme colour variation of one of the species described in this paper. *T. bifrons*, for instance, is a species with a striking variability with respect to the mesonotal and abdominal patterns, and there are also specimens known which have the mesonotal spot restricted to the area behind the suture.

The author recorded several males and females from S. NIGERIA: Ibadan, and from the GOLD COAST.

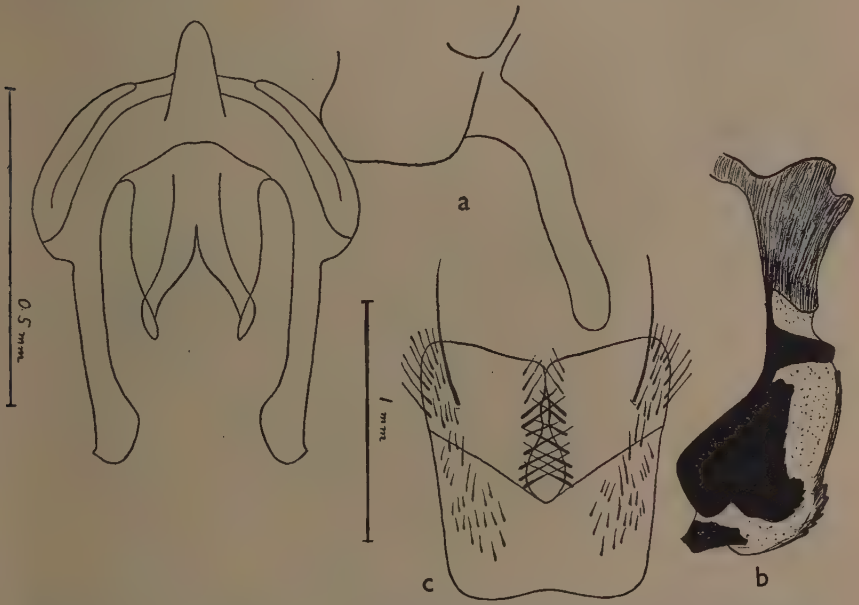

FIG. 17.—*Tricyclea cockbilli* sp. n. (*a*) Cerci and paralobi in frontal view; (*b*) phallosome; (*c*) fifth sternite.

16. **Tricyclea currani** sp. n.

The only male specimen before me is easily recognisable by a sharply defined mesonotal spot which extends from the anterior border to the roots of the last dorsocentral bristles. It is enlarged posteriorly and therefore forms a triangular vitta with a truncated tip. The hypopygium shows some similarity to that of *T. bivittata*, but the paralobi are terminally rounded.

Male.—Eyes touching, upper facets enlarged and fairly well demarcated from the small ventral ones. Frons linear in the middle, triangular below, yellow-brown like the face. Parafrontalia and parafacialia slightly dusted and beset with several fine setae, *iv* long and thick, *ev* wanting, two pairs of proclinate bristles on the ocellar triangle, 6–7 *paf*, facial ridge with a row of black bristles on the lower half; vibrissa long, peristome with a row of bristles, and bucca with black hairs, the last about one-third of the eye-length; proboscis and palpi yellow, the latter narrow, only very slightly enlarged terminally.

Thorax with a mesonotal vitta as described above, otherwise orange dorsally and yellow-brown laterally; $ac = 3 + 3$, $dc = 2 + 4$, $ia = 1 + 3$, $ph = 3$, $h = 3$, $prs = 1$, $n = 2$, $sa = 3$, $sc = 6\text{–}7 + 1$, $st = 1 : 1$, one long and one shorter *pp* and *pst*. Pro- and poststigma yellow. Wings with two costal spots. The basal one covers the whole subcostal cell; the terminal one is separated from the first by a broad, light space and covers about the last third of r_{2+3}; costal spine short but distinct, r_5 dorsally with setae up to *r–m*, alar declivity with fine pale hairs; squama broad, tinged with brown, haltere yellow. Legs yellow-brown, fore-tibia with several short and indistinct *ad* and a long submedian *pv*; mid-tibia with a submedian *av* and *ad*, two *pv*; hind-tibia with two *pd* and *ad* as well as one submedian *av*.

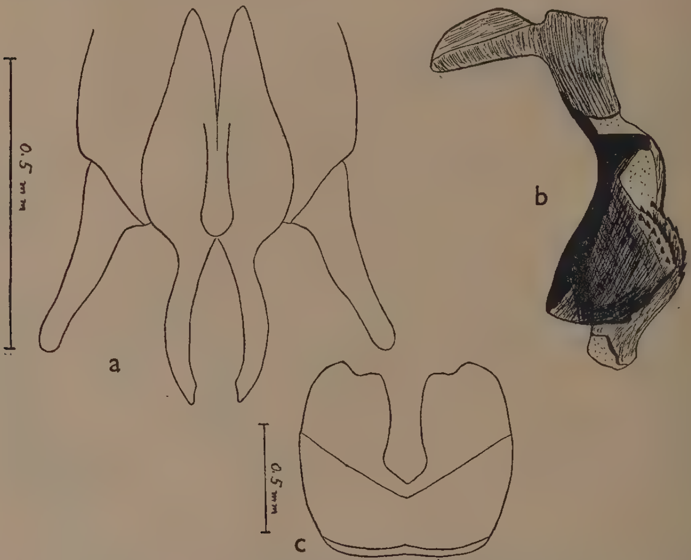

FIG. 18.—*Tricyclea currani* sp. n. (*a*) Cerci and paralobi in frontal view; (*b*) phallosome; (*c*) fifth sternite.

Abdomen with the last two segments totally dark brown, the third with a dark posterior band which is triangularly widened in the mid-line. Hypopygium (fig. 18) with curved and terminally truncated cerci, paralobi finger-shaped.

Length.—6 mm.

Female.—Unknown.

Biology.—Nothing known.

Distribution.—One male from BELGIAN CONGO: Faradje, xi.1912 (*Lang and Chapin*). The species is named in honour of Dr. C. H. Curran, curator of the American Museum of Natural History, New York. Type in the collection of that museum.

17. *Tricyclea diffusa* Malloch.

T. diffusa Malloch (1929) is based on a single male from TANGANYIKA TERRITORY: Amani. It was lost during the war. Villeneuve (1936) undoubtedly redescribed it as *T. ornatipennis*, from several males and females from the Congo area and from Nigeria. It is probable that Séguy's *T. dorippa* (1941) from the Ivory Coast also belongs to *T. diffusa*, but this can only be determined by checking the type.

I have before me four female specimens from Liberia, which I refer to *T. diffusa*. They are characterised by a very extended, glossy black pattern which covers the whole dorsum of the thorax leaving only the shoulders, the postalar area and the extreme tip of the scutellum, yellow or brown. The pleura are more or less darkened but the marks are ill-defined and variable. The abdomen shows very broad black bands which cover two-thirds or more of the third and fourth tergites. In one female these tergites are totally black, but the last tergite always shows two distinct black apical spots. The wing pattern is very characteristic. There is only one ill-defined, dark-brown costal spot which extends from the middle of the subcostal cell to the tip, but is basally widened forming a more or less distinct cloudy extension which reaches *r–m*. The remaining part of the wing is tinged with brown. The legs are yellow brown, but the apical parts of the last two femora and corresponding tibiae as well as the tarsi are more or less darker brown.

I have no doubt that these females before me really belong to *T. diffusa*, but I do not wish to select from them a neotype to replace the lost holotype, as I believe that this should be done with a male specimen from the Kilimandjaro area.

Length.—7–8 mm.

Biology.—Nothing known.

Distribution.—Probably distributed from LIBERIA through CENTRAL AFRICA to TANGANYIKA. The Liberian specimens before me are from Banja, x. 1926, and from Robertsport, x–xi. 1943.

18. *Tricyclea du* Curran.

This species is in general appearance very similar to *T. similis*, although the hypopygium is different and the costal area totally brown. At the most, a linear lighter spot is detectable behind the subcostal cell, and the basal part is a little lighter brown up to *sc*. I have the single male holotype before me and one female, but I believe that the single female type of *T. confusa* Curran (1931) also belongs to this species, being a relatively lightly coloured specimen. Curran himself synonymised Malloch's (*nec* Curran's) *T. bivittata* (1929) with his *confusa*.

With the exception of the wing pattern and the shape of the hypopygium (fig. 19), I cannot detect any characteristics which seem to be constant enough to justify their being used as distinguishing features from *T. similis*. The black pattern of the holotype of *du* has the same form as that of *similis*, but it is ill-defined and lightened between the *ia*, so that the mesonotal pattern here consists of two black vittae. The scutellum has a black disc and a yellow margin as in *T. similis*. A female before me which I place in the species *T. du* has exactly the same pattern as *similis*, whereas the single holotype of *confusa* has a reduced pattern. In the latter, only the anterior part of the mesonotum is black, whereas the hind part and the disc of the scutellum are dark brown. This pattern, however, gives the impression of not being fully developed, for if the dark brown parts are taken as black, a pattern identical with that in *similis* is obtained.

It is curious that the hypopygium of *T. du* shows a striking resemblance to that of the South African *T. bivittata* Curran which Malloch confused with *T. du*. Another relationship is given by the tendency in *du* of the mesonotal pattern to dissolve into two longitudinal vittae. Otherwise, *T. bivittata* is bigger and much lighter coloured than *du*. These two species cannot therefore be confused with respect to their general appearance. More material will have to be examined to determine whether there is a closer relationship which would make it necessary perhaps to regard these two forms as subspecies.

Length.—6–7 mm.

Biology.—Nothing known.

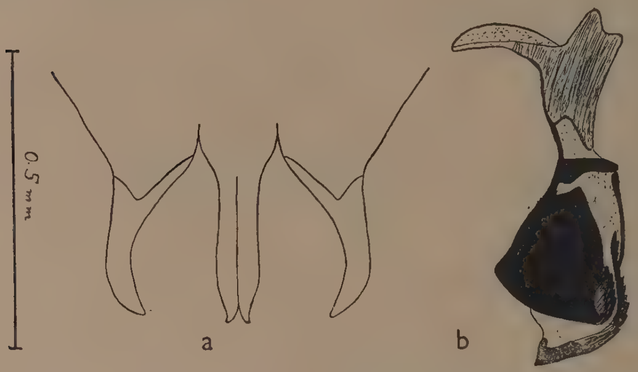

Fig. 19.—*Tricyclea du* Curran. (*a*) Cerci and paralobi in frontal view; (*b*) phallosome.

Distribution.—Only known from Liberia. The male holotype of *du* comes from the Du River, the female holotype of *confusa* from Reppo's Town, but Curran has recorded another female from the Du River also. The other female mentioned above was collected at Liberia: Robertsport, xi.1943.

19. *Tricyclea bivittata* Curran.

A characteristic species with two broad longitudinal vittae on the mesonotum and the costal area behind *sc* totally brown or only very narrowly interrupted behind the subcostal cell.

Male.—Eyes touching, inner facets a little larger than the outer ones but not demarcated from them; ocellar triangle and upper parafrontalia black brown, lower part of frons and face bright yellow and orange; *iv* and one pair of proclinate *oc* well-developed, *ev*, *f* and *fo* wanting, 6–7 *paf*, parafrontalia and upper parafacialia with a row of short black setae, lower half of facial ridge bristled; vibrissa long; peristome with a row of bristles, one of which is almost as long as the vibrissa; buccae about one-third of eye length, beset with black hairs; palpi yellow, terminally dilated; proboscis dark brown.

Thorax with two broad longitudinal black vittae which cover the area between the *ia* and *ac* but are ill-defined; posteriorly they do not reach the scutellum; remaining thorax yellow-orange. Chaetotaxy: $ac = 3 + 3$, $dc = 2 + 4$, $ia = 1 + 3$, $ph = 3$, *h* = 3, *prs* = 1, *n* = 2, *sa* = 3, *sc* = 5–6 + 1, *st* = 1 : 1, *pst* and *pp* consisting of one long and one to two shorter and thinner bristles. Pro- and poststigma yellow, post alar declivity with pale hairs. Wings with the costal area behind *sc* totally dark brown, or there is a more or less distinct narrow hyaline stripe behind the subcostal cell, basal costal area hyaline or at least distinctly lighter brown; veins dark brown, costal spine wanting, r_5 dorsally with setae up to *r–m*, squama broad, light brown, haltere yellow. Legs yellow, tips of the last two femora and tarsi slightly darkened; fore-tibia with 2 *ad* and one long submedian *pv*; mid-tibia with one *av*, *ad* and 2 *pv*; hind-tibia with 2 *ad* and one submedian *av*.

Abdomen yellow-brown, second tergite with a narrow, and third and fourth tergites with broad, black marginal bands, covering one-third to one-half of the segment; last tergite with paired apical spots. Hypopygium (fig. 20) with strong cerci which have a small terminal tooth; paralobi as long as the cerci, terminally bent and pointed.

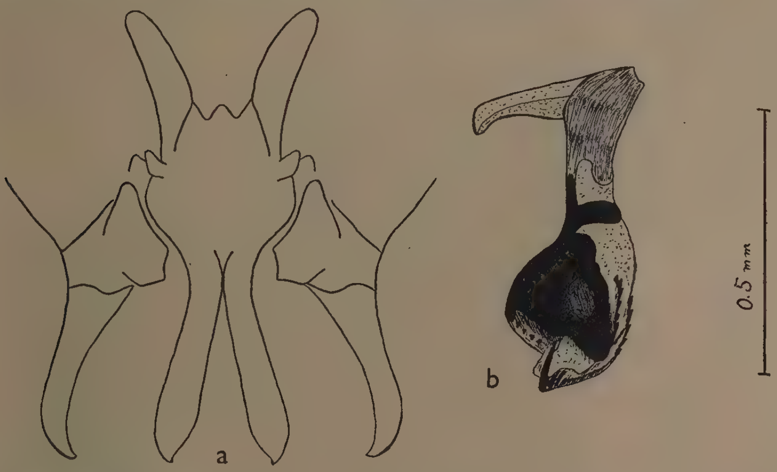

FIG. 20.—*Tricyclea bivittata* Curran. (*a*) Cerci and paralobi in frontal view; (*b*) phallosome.

Female.—Frons at the vertex a little more than one-third of the eye length, slightly narrowed in the middle; upper part of parafrontalia and ocellar triangle dark brown, otherwise orange; eye facets as in the male; palpi a little more dilated. Chaetotaxy consists of *iv*, *ev*, *oc*, *f* and a complete row of *paf*.

Length.—7–8 mm.

Biology.—Nothing known.

Distribution.—Only the typical series is known, consisting of 4 males and 2 females from S. RHODESIA: Salisbury, and CAPE PROVINCE: East London (*leg. Minow*), iii and vi. 1923.

20. *Tricyclea major* Curran.

The largest *Tricyclea* species of which, up to the present, only a single female was known. In the unidentified material, sent to me by Dr. Curran, I discovered a male so that the description can now be based on the male sex. The hypopygium has strikingly enlarged paralobi as in the *Bengalia* species.

Male.—Eyes with the inner facets slightly enlarged but not demarcated; frons at the narrowest part as broad as the ocellar triangle; or about one-tenth of the eye length; ocellar triangle black, upper part of frons red-brown; lower part and face yellow and orange; *iv* long and thick, *ev* short, hardly longer than the postorbital hairs, *f* and *fo* wanting, *paf* reaching the narrowest part of the frons; lower half of facial ridge with bristles, vibrissa long, peristome with bristles, one of which is as usual almost as long as the vibrissa; buccae only about one-quarter of eye length, beset with black hairs; proboscis and palpi yellow, the latter slightly dilated terminally.

Thorax orange without pattern, *ac* = 3 + 3, *dc* = 2 + 4, *ia* = 1 + 3, *ph* = 3, *h* = 3, *prs* = 1, *n* = 2, *sa* = 3, *sc* = 6 + 1, *st* = 1 : 1, *pst* = 2, *pp* = 1. Pro- and poststigma yellow, alar declivity with pale hairs. Wings with the costal area totally brown, a very narrow hyaline stripe behind the tip of *sc*, remaining wing brownish tinged, veins dark brown, costal spine distinct; dorsal setae on r_5 slightly surpassing *r–m*; squama yellow-brown, very broadly truncated; haltere yellow. Legs yellow, hind-tibia and tarsi slightly darkened; fore-tibia with 2 short *ad* and a long submedian *pv*; mid-tibia with one *av*, *ad* and two *pv*; hind-tibia with 2 *ad*, *av* and one submedian, indistinct *pd*.

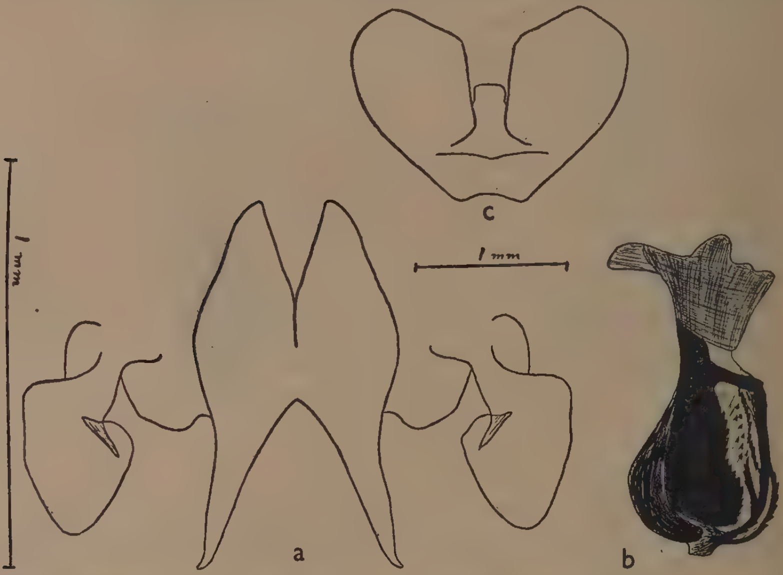

FIG. 21.—*Tricyclea major* Curran. (*a*) Cerci and paralobi in frontal view; (*b*) phallosome; (*c*) fifth sternite.

Abdomen yellow-orange, second tergite with a narrow band, third tergite with a marginal band covering about one-fourth of the segment, fourth tergite with a very broad band which is widened in the middle and covers there about three-quarters of the segment; hind tergite with two large apical spots. Hypopygium (fig. 21) with slender cerci having hook-shaped tips, paralobi broadly triangular with rounded angles; phallosome heavily sclerotised, with wing-like diverging protrusions opposite the vesicae.

Female.—The female specimen before me, representing the holotype, has the frons at the vertex slightly more than one-third of eye length, and a little narrowed towards the middle; upper part of parafrontalia and ocellar triangle black brown, otherwise orange; *iv*, *ev*, divaricated *oc*, *f* and one *fo* long and strong; *paf* consist of 6 long and thick and

6 short and thin bristles; hairs and bristles of the face as in the male. Thorax coloured and bristled as in the male, but *dc* asymmetrically developed, four left and three right; only one *pp* and *pst*. The chaetotaxy on the legs is slightly different from that on the male, consisting of only two longer *ad* on the fore-tibia, and slightly longer bristles on the hind-tibia. In spite of these differences, which lie within the known variability, I believe that the above described male belongs to *T. major*.

Length.—9–10 mm.

Biology.—Nothing known.

Distribution.—LIBERIA: Paiata (♀) and Bendu, Robertsport (♂), x.1926 and xii.1943.

21. *Tricyclea spiniceps* Malloch.

I have not seen this species. The two typical specimens, one male and one female, were preserved in the Zoological Museum of Hamburg, where they were lost during the last war.

Male and female are described as testaceous-yellow with the following parts black: upper half of occiput, posterior third or more of frontalia, mesonotum except lateral margin, a mark on hypopleura, an apical fascia on the third abdominal tergite, another on the fourth, both of which are widened in the middle and do not extend to the lateral extremities, and paired apical spots on the last tergite. Costal area brown from *sc* up to the tip, a subhyaline streak more or less distinct "along costal vein beyond apex of first vein." Male frons fully three times as wide at the narrowest point as distance across posterior ocelli. *iv* present in male and both verticals developed; upper half of parafacialia with black setae, buccae with black hairs; palpi slightly club-shaped in both sexes. Chaetotaxy of thorax as usual. Fifth abdominal sternite with a deep incision, inner corner blackened, with a blunt tooth.

Length.—7–8 mm.

Biology.—Nothing known.

Distribution.—NIGERIA: Buea.

D. SYSTEMATIC CATALOGUE.

Hemigymnochaeta Corti, 1895.

Corti, Ann. Mus. Stor. nat. Genova **35**: 142 (gt. *lutea* Corti).

Auchmeromyiella Townsend, 1918, Ins. Inscit. menst. **6**: 154 (gt. *angola* Towns.).

Tricyclodes Curran, 1927, Ann. Mag. nat. Hist. (9) **19**: 525 (gt. *pallens* Curr.).

1. *unicolor* (Bigot), 1887, Bull. Soc. zool. Fr. **12**: 608.
    - *lutea* Corti, 1895, Ann. Mus. Stor. nat. Genova **35**: 142.
    - *flaveola* (Bezzi), 1908, Ann. Soc. ent. Belg. **52**: 383.
    - *clara* Curran, 1931, Amer. Mus. Novit. **506**: 11.
    - ? *flavella* (Villeneuve), 1937, Bull. Mus. Hist. nat. Belg. **13** (35): 3.
    - *flaveola* Séguy (*errore*), 1946, Encycl. Ent. (B) 2. Dipt. **10**: 35.
2. *bequaerti*, Curran, 1931, Amer. Mus. Novit. **506**: 14.
3. *varia* (Hough), 1898, Nat. sci. Philad. **1898**: 178.
    - *angola* (Townsend), 1918, Ins. Inscit. menst. **6**: 154.
    - *difficilis* (Curran), 1927, Ann. Mag. nat. Hist. (9) **19**: 526.
    - *pallens* (Curran), 1927, ibid. (9) **19**: 525.

tridentata (Villeneuve), 1936, Bull. Mus. Hist. nat. Belg. **12** (4) : 3.

4. **laticeps** sp. n.

5*a*. *liberia liberia* Curran, 1931, Amer. Mus. Novit. **506** : 12.

5*b*. *liberia* **orientalis** ssp. n.

6. *gracilis* Séguy, 1933, Mem. Estud. Mus. Zool. Univ. Coimbra (1) **67** : 73.

7. *roubaudi* Séguy, 1941, Encycl. Ent. (B) 2, Dipt. **10** : 34.

?*fuliginosa* (Villeneuve), 1936, Bull. Mus. Hist. nat. Belg. **12** (41) : 2.

8. *apicifera* Curran, 1931, Amer. Mus. Novit. **506** : 12.

9. *mitis* Curran, 1931, ibid. **506** : 13.

Species incert.

10. *ornata* Séguy, 1933, Mem. Estud. Mus. zool. Univ. Coimbra (1) **67** : 76.

Tricyclea Wulp, 1884

Wulp, C.R. Soc. ent. Belg. **28** : 293 (gt. *ferruginea* Wulp).

Zonochroa Brauer & Bergenstamm, 1891, Musc. Schiz. **2** : 87 (gt. *fasciata* Macq.).

1. **nana** sp. n.

2. *ochracea* Séguy, 1938, Encycl. Ent. (B) 2 Dipt. **9** : 22.

3. *semicinerea* Bezzi, 1908, Boll. Soc. ent. ital. **39** : 77.

palliventris Curran, 1927, Ann. Mag. nat. Hist. (9) **19** : 516.

?*analis* Malloch, 1929, ibid. (10) **3** : 559.

4. *claripennis* Séguy, 1933, Mem. Mus. zool. Univ. Coimbra (1) **67** : 74.

5. **patrizii** sp. n.

6*a*. *fasciata fasciata* Macquart, 1843, Mem. Soc. R. Sci. Lille **1842** : 290.

exarsa Brauer and Bergenstamm, 1891, Denkschr. Akad. Wien. **58** : 178.

evanida Villeneuve, 1922, Trans. ent. Soc. Lond. **1921** : 519.

kasatana Curran, 1931, Amer. Mus. Novit. **506** : 6.

6*b*. *fasciata ferruginea* Wulp, 1884, Bull. Soc. ent. Belg. **1884** : 294.

7. *resurgens* Villeneuve, 1932, Rev. Zool. Bot. afr. **21** : 284.

8. *latifrons* Curran, 1927, Ann. Mag. nat. Hist. (9) **19** : 517.

9. *unipunctata* Curran, 1927, ibid. (9) **19** : 518.

? *pterostigma* Bezzi, 1914, Boll. Lab. zool. Portici, **8** : 290.

liberia Curran, 1931, Amer. Mus. Novit. **506** : 8.

? *gracilis* Séguy, 1933, Mem. Mus. zool. Univ. Coimbra (1) **67** : 73.

10. *nigroseta* Curran, 1927, Ann. Mag. nat. Hist. (9) **19** : 522.

11. *similis* Curran, 1931, Amer. Mus. Novit. **506** : 10.

12. *bifrons* Malloch, 1929, Ann. Mag. nat. Hist. (10) **4** : 117.

? *verticella* Villeneuve, 1922, Trans. ent. Soc. Lond. **1921** : 521.

binotata Malloch, 1929, Ann. Mag. nat. Hist. (10) **4** : 116.

? *bipartita* Séguy, 1938, Encycl. Ent. (B) 2 Dipt. **9** : 62.

13. *perpendicularis* Villeneuve, 1922, Trans. ent. Soc. Lond. **1921** : 522.
    distigma Curran, 1927, Ann. Mag. nat. Hist. (9) **19** : 520.
14. **cockbilli** sp. n.
15. *semithoracica* Villeneuve, 1922, Trans. ent. Soc. Lond. **1921** : 520.
16. **currani** sp. n.
17. *diffusa* Malloch, 1929, Ann. Mag. nat. Hist. (10) **3** : 560.
    ornatipennis Villeneuve, 1936, Bull. Mus. roy. Hist. nat. Belg. **12** (4) : 9.
    ? *dorippa* Séguy, 1941, Ann. Soc. ent. Fr. **109** : 126.
18. *du* Curran, 1931, Amer. Mus. Novit., **506** : 8.
    bivittata Malloch (*nec* Curran), 1929, Ann. Mag. nat. Hist. (10) **3** : 557.
    confusa Curran, 1931, Amer. Mus. Novit. **506** : 9.
19. *bivittata* Curran, 1927, Ann. Mag. nat. Hist. (9) **19** : 523.
20. *major* Curran, 1931, Amer. Mus. Novit. **506** : 7.
21. *spiniceps* Malloch, 1929, Ann. Mag. nat. Hist. (10) **3** : 557.

Species incert.

22. *bicolor* Bezzi, 1908, Ann. Soc. ent. Belg. **52** : 383.
23. *decora* Séguy, 1933, Mem. Mus. zool. Univ. Coimbra (1) **67** : 73.

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THE RELATIONSHIP OF *COLIAS CROCEUS* (FOURCROY) AND *COLIAS ELECTO* (LINN.).

By F. V. L. Jarvis, B.Sc., F.R.E.S.

Manuscript received 23rd September, 1952.

(Read 6th May, 1953.)

With 1 Plate (coloured) and 7 Text-figures.

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Introduction.

The present paper describes recent comparative work by the author on *Colias croceus* (Fourcroy) and *Colias electo* (Linn.). An examination of the results provides good evidence for considering these two Coliad butterflies as separate species. As is well known, this question of status is of long standing, opinion at present probably regarding *C. croceus* as a subspecies of *C. electo*. Seitz, writing of *C. croceus*, states: "According to the rule of priority we have to deal with this species under its old name, *croceus* [= *edusa* (Four.); *hyale*

(Esp.); *helena* (H. Sch.).] is most likely a local form of *electo* (Linn.), which is distributed all over Africa and already described in 1763."

Talbot (Junk, *Lep. Cat.*, Part 66: 469) treats *croceus* as a subspecies of *electo*, with *C. electo electo* (L.) becoming the nominotypical form by priority of nomenclature. This classification is followed by Dr. Van Son in *The Butterflies of South Africa* (1949), where it is stated that *electo electo* occurs in the nominotypical form only in South Africa, but is represented by several races in Ethiopian and Northern Africa (*electo hecate* group: Strecker and Berger), in Europe by *croceus* and in Southern Asia to Central China by *electo chinensis* (Verity), which is presumably synonymous with *C. fieldii* (Men.). In 1940 M. L. Berger, from comparison of genitalia, androconia and constant pattern differences, considered that *croceus* and *electo* were separate species. Dr. B. J. Lempke (1944) held the same view in regard to *croceus*, *electo* and *fieldii*. Berger analyses the African subspecies of *electo* as follows:

electo electo—South Africa.
electo meneliki—Abyssinia.
electo hecate—West Africa: Congo.
electo pseudohecate—Belgian Congo; Kenya; Tanganyika; Abyssinia; Somaliland.

C. electo meneliki and *C. electo pseudohecate* were described as new forms by Berger in 1940; *hecate* was described by Strecker at the end of the nineteenth century, and *electo* is the original form according to Linnaeus. For the sake of brevity in the ensuing text the distinctive names only will be used, namely "*electo*" for "*electo electo*"; "*pseudohecate*" for "*electo pseudohecate*," etc.

The African forms, particularly near the Equator, are found at altitudes where the climate approximates to the warmer parts of the temperate zone. Being separated by barriers of unfavourable tropical lowland, they may be expected to show divergence during evolution from a common ancestor.

Classification has perforce been made up to the present from the comparison of imaginal characteristics, but it is permissible to suggest that critical examination of all stages might alter the conclusion, particularly in the Coliads, where visible differences between species are often slight. If two forms show constant differences at all stages when reared in the same environment, there seems a logical basis for considering these to have acquired sufficient divergence in evolution to be regarded as separate species.

METHOD.

After preliminary experiments, using the air mail postal service so as to keep within the limit of 6 days before eggs hatched in transit, it was found possible in 1951, to raise *C. electo* in England from eggs collected by Mr. A. Duke near Cape Town. I was able to compare my results with the comprehensive description already made by Mr. Gowan Clarke in Port Elizabeth. Later in 1951, by the same postal method, Mr. Clarke successfully reared *C. croceus* in South Africa, using half the eggs laid by one female whilst I reared the remainder in Sussex as a control. We thus had both forms growing in England and South Africa and were able to make critical comparisons. In neither case did the foreign environment cause any definite alteration in the colour or pattern of the imagines. Mr. Clarke attempted a pairing, which will be described later, between *croceus* and *electo*.

Detailed and illustrated descriptions were made of all stages. Genitalia preparations were made of *croceus*, *electo*, *pseudohecate* and *fieldii*. Androconial scales were examined in these four forms, which are all members of a group of Coliads in which the males have a patch of scent scales (androconia) at the proximal end of the costal area (upper surface) in advance of nervure 8 of the hind wings. The main issue at the outset of the study was between *croceus* and *electo*, the only forms whose complete life-history was then known with accuracy, but recently (May, 1952) I have been able to rear *pseudohecate* in England. There are constant differences at all stages from both *C. electo* and *C. croceus*.

COMPARISON BETWEEN *C. croceus* AND *C. electo*.

Distribution.

The general distribution of *C. croceus* is well known, but if the habitat of a migratory species is defined as the zone in which it is capable of existing throughout the year, the area is considerably reduced. Experiments made by the author during the winter of 1951/52 on the resistance of *croceus* larvae to cold and humidity variations suggest that an average minimum temperature of 50° F., with low humidity, for not more than two months is about the limit for survival. These conditions would reduce the wintering area to the Southern and Eastern littoral of the Mediterranean, with the possible inclusion of sheltered portions of the Northern shore and islands. There is an eastward extension to Persia and Iraq, from which region Col. H. D. Peile has reported *croceus* in all months of the year except January, adding that the February specimens were small. Obviously the species is indigenous in this area.

C. electo is distributed throughout the Union of South Africa, but the difficulties of field work being much greater than in Europe, comprehensive mapping has not been possible. Northwards from Rhodesia there appear to be forms transitional to *hecate* and *pseudohecate*. These two subspecies occur in suitable highlands of the Congo, Central and Eastern Africa. Further to the north-east subsp. *meneliki* is found in Abyssinia, but the desert barrier of Upper Egypt seems to prevent further northward movement of *electo* or southern migration of *croceus*.

Pattern.

Superficially there is a similarity in appearance between *croceus* and *electo*, but examination of series reveals constant differences. *C. electo* is more variable in size in individuals from one locality, between series from different stations, and in wet and dry season broods. In some measure this may be caused by fluctuation in the nutritive value of food plants, which normally are vetches, although the larvae feed readily on lucerne and clovers. Probably there is little difference in average wing span, but *electo* is the more slender butterfly. The apical angle of the fore wings is more acute, whilst the hind wings are relatively smaller than in *croceus*. Ground-colour in *electo* is a deep dull orange, somewhat paler and more yellow in the female, with a cerise lustre particularly noticeable in the male. *C. croceus* is bright orange yellow, whilst the occasional faint lustre in the males is definitely lilac. Fore wing black bands (male) dusted with yellowish scales are practically identical in outline in both forms. The female pattern of yellow marginal spots is similar, but the black marginal area in the fore wings of *electo* extends further into the disc, with black scaling on the nervures reaching, in some specimens, to the discoidal spot. Irroration of basal and costal grey scaling is more extensive in females of *electo*.

Detailed description of the fringes appears to have had little attention up to the present, but examination of the four forms, *croceus*, *electo*, *pseudohecate* and *fieldii*, showed points of difference which are described in detail.

C. croceus, in both sexes and in the white female ab. *helice* (Hb.), always shows a characteristic chequering of dull pink against an ochre yellow inner border (cream in *helice*). This applies to the upper surface of the fore wings. Pink disappears at the hinder angle, and reappears as the dominant colour near the hinder angle of the hind wings. Fringes on the under surface are pink, except for a yellow or cream zone at the hinder angle of the fore wings.

In *electo* the upper surface fore wing fringe is almost completely deep dull pink, with only a trace of chequering of lighter pink extending to the hinder angle, which is dull yellow. Hind-wing fringes are pale dull pink, somewhat yellower near the costa; under surface is dull pink. Both sexes are similar. In *pseudohecate* fringes are uniformly brown pink on all wings (both sexes), becoming paler and more orange on the hind wings. The transition to orange-pink takes place at the hinder angle of the fore wing. Under-surface fringes pink. *C. fieldii* resembles *C. electo* except that the pink is tinged with orange. There is a trace of chequering on the fore wings.

It is noteworthy that the chequered fore-wing fringe is clearly shown in the *hyale/erate* group.

In all four forms the tibio-tarsal portion of the legs is pink; palest in *electo*, deepest in *pseudohecate*.

The under-surface wing pattern is similar in both *croceus* and *electo*, but *croceus* shows the more brilliant ground-colour. The hind-wing discoidal spots (Plate 1, figs. 8, 16) show a constant difference, which was described by Berger in 1940. Besides being larger, in *croceus* the white single or twin spot is enclosed by a dark purplish brown border, surrounding this is a paler zone and finally a perimeter of dark brown, giving the appearance of concentric rings. In *electo*, *hecate*, *pseudohecate* and *fieldii* the white discoidal spot has only the inner dark border shading outwardly to lighter brown, with no trace of an outer dark line. The double outline occurs in the *hyale/erate* group, in *C. romanovi* (Central Asia), *C. myrmidone* (S. E. Europe to S. Russia) and in *C. eurytheme* (N. America).

The white forms of the female show a marked pattern difference. In ab. *aurivilliusi* (Keferst.) of *electo* the basal irroration on the upper surface of the fore wings is sooty grey with a well-defined boundary extending, in some specimens, almost to the discoidal spot. Irroration on the hind wings is neutral grey without the bluish or greenish tinge usually seen in ab. *helice* (Hb.) of *croceus*. The most characteristic distinction is in the hind wing discoidal spot (upper surface). In *aurivilliusi* this is greyish white, occasionally tinged with pale yellow. In *helice* the spot is usually orange or yellow and rarely cream or white. Mr. A. Duke, who has examined numbers of *C. electo* in S. Africa, states that he had never seen any specimens of *aurivilliusi* in which there was any yellowish colouring in the hind-wing discoidal area apart from the spot, or any forms which could be regarded as intermediates between *aurivilliusi* and the orange type. Except in the whitest forms of *helice*, which are relatively uncommon, there is a slight shading of yellow or orange in the disc of the hind wings (upper surface), and pale yellow specimens occur frequently in a population of *helice*.

Behaviour and seasonal variation.

Both *croceus* and *electo* maintain a succession of broods throughout the year with no recognizable diapause at any stage. *C. croceus* becomes plentiful in the summer of favourable years and migrates northwards across Western Europe. *C. electo* increases in numbers in the wet season, which for the greater part of South Africa is from December to March ; but it is the potentiality of migration on a considerable scale which appears to form a distinction between *croceus* and *electo*. From African field observations, which admittedly are scanty, there is little to suggest that the *electo* sub-group is prone to migrate to any extent. Dr. Van Son wrote me that the distribution of *electo* is very continuous throughout the Union south of the Limpopo river, but becomes extremely scarce in S. Rhodesia, except around Umtali and the Vumbu mountains. Specimens from these northern localities appeared to be somewhat transitional to *C. hecate*. He added that never in his experience in S. Africa had he witnessed any mass migration of *electo*, although some small numbers have been observed in the migratory flights of *Belenois aurota*.

C. electo of the summer broods in the *summer* rainfall area are larger and more brilliant than the winter (dry season) specimens, with less irroration of grey scales on the undersides. In the Western Cape Province (which has a *winter* rainfall with cool weather) the typical winter form is the smaller, with a darker and duller underside due to the admixture of greyish scales. The white female (*aurivilliusi*) is stated to be more plentiful in the dry season, which, with the exception of Western Cape, has the lower average temperature. Experimentally I found a similar result with *C. croceus* reared in England at low temperatures during the winter. The imagines were smaller and duller in colour than in summer broods whilst the undersides of the hind wings were thickly sprinkled with dusky scales.

Life history.

(1) *Duration*.

The life cycle is approximately the same length in each species, as can be seen from the figures averaged from a number of experimental rearings :

Duration in days.

	Egg stage.	Larval period.	Pupal period.	Total.
C. croceus (average temperature of 65° F.) .	7·5	27 to 35 (av. 31)	10	48·5
C. electo (average temperature of 70° F.) .	7	25 to 29 (av. 27)	7	41

Above 55° F. *croceus* conforms well to Van Holt's Law, which states that for every 10° C. (or 18° F.) rise of environment temperature, metabolic activity is doubled. If this correction is applied to the *croceus* figure of 48·5 days to give an equivalent duration at 70° F., the result is 41·5 days, which is in close agreement with the observed value for *electo.*

(2) *Winter Experiments with* C. croceus *Larvae.*

During the winter of 1951/52 I carried out experiments on *croceus* to determine, if possible, the degree of resistance of the larvae to English winter conditions on the Sussex coast. As the result of a pairing in late September from the F_1 generation raised from a wild female taken early in August, some 200 larvae hatched on about 25th October. The original intention was to keep these outdoors in an open zinc cage on pots of lucerne, but losses from earwigs and dew-drenched food caused a change of plan. The pots with 130 surviving larvae in early November were brought into an unheated room facing north near an open window. Larvae grew at different rates, but after the middle of January, mortality, which had been low, increased rapidly. There was no sign of dysentery, but from the gradual onset of feebleness it was suspected that death was caused by some form of internal congestion. As larvae neared the end of the final instar they were kept at 55–60° F., and this temperature was maintained in the pupal period. Average temperature during larval existence was 47° F., calculated from daily readings. Ignoring several pupal deaths, the following emergences were obtained :

			Larval stage.
6 males.	9th to 15th Feb.	(pupated 14th to 22nd Jan.)	81–89 days
1 female.	7th March	(,, 20th Feb.)	118 ,,
1 male.	9th March	(,, 25th Feb.)	123 ,,
1 male.	23rd March	(,, 12th March)	139 ,,

The male emerging on 23rd March was a marked contrast to the earlier butterflies, being comparable in size and colouring to summer specimens. During the last instar it had the advantage of strong sunlight and healthier lucerne.

One adult larva died on 23rd March, after an existence of 150 days.

The final result, therefore, was 8 males and 1 female, that is, 7 per cent. of the initial 130 larvae. Males seemed to have a higher potentiality of survival, as three out of five dead pupae were recognizably of this sex. It is interesting to record that on 5th January (after 72 days) 97 larvae in instars 3, 4 and 5 were alive, but by 14th Feb. (112 days) the figure had fallen to 21. Finally only 3 of these pupated, as noted above (20th, 25th Feb. and 12th March).

On 7th Jan. 30 larvae in instars 3, 4 and 5 were placed outdoors on clover and lucerne growing in a sheltered corner of the garden. They were protected only by a sheet of glass supported on bricks. The ensuing six weeks were cold (av. 38° F.) with considerable frost but 5 larvae survived the period, but all died eventually, the last survivor being the 150-day specimen. There would appear to be a variable resistance to cold.

Probably the most significant result is the indication of a state of inertia representing a stage towards diapause. The F_1 generation showed an average larval period of 30 days at 63° F. in August and September. If this figure is corrected for 47° F. the theoretical period for the winter larvae should have been 53 days. The actual figures were between 81 and 150 days. It should be remembered that the last portion of the 5th instar was hastened by higher temperature, so that the period would have been still longer if kept throughout at 47° F. It appears from these results that the prolonged effect of environment temperature below 50° F. is to induce a lethargy which cannot be described as true diapause but as a phenomenon of similar nature. Later in 1952 further results were obtained in support of this view. From a yellow female *croceus* 35 eggs were laid between 21st and 23rd August. Hatching took place between 30th August and 4th September. Pupation was completed from 3rd October to 10th October, the larvae having been kept at an average temperature of 56·5° F. (range of fluctuation 5°). This gave an average larval period of 35 days, which is in close agreement with the figure of 30 days at 63° F. Total emergence, 20 ♂, 15 ♀.

A female ab. *helice* between 24th September and 3rd October laid 157 eggs. Hatching took place between 11th and 22nd October, and pupation from 7th to 27th December, giving a mean larval period of 61·5 days at an average temperature of 57° F., which was nearly double the time for the earlier September brood. Both sets of larvae were raised as nearly as possible in identical conditions of food and temperature. The total emergence was 77 ♂ : 37 ♀ (type) : 36 ♀ *helice*. All specimens were of average size, except for 5 dwarfs.

A tendency for reduction in extent of marginal bands was present in both sexes, particularly on the hind wings. Marginal spots in females were smaller than in summer insects. There was a considerable amount of dusky scaling on the hind-wing underside in the majority of cases. In both these experiments *Medicago* and lucerne were used as food-plants. The fact that the December insects were of normal size is an indication that there could have been little deterioration in food value between September and December, so that one has to look for another reason to explain the extended larval period. Temperature was practically the same for the two series. It is premature to form conclusions from these experiments, but I am inclined to the view that winter larvae in *C. croceus* have inherently a slower growth-rate than those hatched in summer, quite apart from the retarding that would be caused by lower temperature. This supports the suggestion of a lethargy phenomenon, but in the 1951/52 experiment it would appear that an average of 47° F. must have been too low for healthy survival. It has not yet been possible to test *electo* in the same way.

(3) *Egg Laying and Larval Behaviour*.

The two species show no appreciable difference in method of egg laying, larval behaviour and choice of pupal sites, except that *croceus* larvae wander farther before settling down to pupate.

DETAILED COMPARISON OF THE STAGES.

There are a number of constant differences, some of which are illustrated on Plate I. I am much indebted to Mr. Gowan Clarke for a detailed comparison and the loan of his beautiful coloured plates of *C. electo* and *C. croceus*. These paralleled my own observations and drawings, so that I feel there is little doubt about the accuracy of the points at issue. To save space, data are set out in tabular form :

C. croceus.	*C. electo.*
Egg.—0·4 mm. diam × 1·1 mm. high. 20–21 longitudinal ribs; 36–40 cross braces which are fairly well defined. Lustrous yellowish-white when laid, changing to deep orange salmon with bright yellow extremities. Upward taper starts 1/3 from the base. (Plate I, fig. 9.)	0·35–4·0 mm. × 1·1 mm. 18–22 longitudinal ribs; 28–35 faint cross braces. Cream-white when laid, changing to salmon with dull yellow extremities. Shape elliptical, in which respect there is a difference from *croceus*. (Plate I, fig. 1.)
Larva.—1st instar; 1·5 mm. on emergence; pale brown with black head, and white setae on black moles; setae above spiracles spoon-shaped; setae on sides flattened; on prolegs and ventral surface pointed. Growth to 3·5 mm. (Plate I, figs. 10 and 11.)	1·5 mm. Pale brown, slate or olive with black head. Setae white on black moles. Setae above spiracles half the size of those in *croceus*; otherwise as in *croceus*. Growth to 2·75 mm. (Plate I, figs. 2 and 3.)
2nd instar.—Body and head greenish drab. Setae white and pointed; 22 above spiracle on each side on 7th segment, 15 below. The appearance is hairy. No spiracular line. Growth to 6 mm. (Plate I, fig. 12.)	Slate grey inclining to green in some specimens; head brown. 15 short white setae above spiracle on 7th segment; 12 below. Velvety appearance. Thin pale spiracular line. Growth to 5·5 mm. (Plate I, fig. 4.)
3rd instar.—Colour deep green. Setae of medium length, pointed and *whitish*; about 32 above and 25 below spiracle on 7th segment. Cream spiracular line. Growth to 9·5 mm.	Colour dull green. Setae short, *black* and pointed above; white below spiracle on 7th segment; 32 above, 21 below. Lower setae flattened. Growth to 9 mm.
4th instar.—Colour deep green. White spiracular line with a salmon-red blotching varying in size between individuals. More setae in *croceus*, particularly between the spiracles. All setae whitish. Growth to 16 mm.	Colour olive green with white spiracular line. Setae short, black and pointed except on lower surface of segments 1–3, where they are whitish. Growth to 16 mm.
5th instar.—Whole surface of body a deep green shading to a slightly more yellow green on ventral surface. A close pattern of black tubercles set in clear green rings, with a dusky background on the dorsum. Below the spiracular line the tubercles extend on to the prolegs but are more numerous in some individuals. Spiracular line white, clouded on its lower edge with light yellow. A salmon-pink or orange vermilion blotch occurs in the line on each segment behind the spiracles, which are white with a blackish rim. In many larvae there is a black spot on each segment,	Ground-colour yellowish green with an olive tinge. Spiracular line white with pale yellow clouds in many individuals but in a pale variety may be entirely white. Spiracular line may be bordered below with elongated black spots in centre segments or with dark green throughout. In most larvae there is a dark green subdorsal line, generally darker at the centre of the segment and extending almost to the spiracular line as a deep green band. In extreme forms this subdorsal line may be edged with blackish with a whitish zone above, in which cases the dorsum

below the line from segments 3–10. Setae about twice the length of those in *electo*, rising from black tubercles. These setae are more numerous than in *electo* and are white except on the upper surface of the head and dorsum, where the distal ends become blackish. Head yellowish green. There is a pale form of the larva in which ground-colour is a light bluish green; white spiracular line with salmon-pink spot and no yellow. Occasionally in *croceus* the darker dorsal line is faintly visible, but there is no lateral zone of deeper green. Growth to 32 mm. (Plate I, figs. 13, 14.)

is a lighter green than in other types. In an extreme pale type the larva is pale green with a white spiracular line and no further markings. The body is covered with minute black setae set on black tubercles in paler rings. Towards the feet the setae change to white, arising from black tubercles set on dark patches. Spiracles white with blackish rim. Head yellowish green with small black setae, changing to white and becoming longer in the region of the occelli. Growth to 30 mm. (Plate I, figs. 5, 6.)

Pupa.—Very similar in both species, but that of *croceus* is more ventricose and a brighter green when first formed. The rostrum is straight in *croceus* but curves slightly downwards in *electo*. (Plate 1, figs. 7, 15.)

This detailed analysis seems to be the only method of defining these constant differences, which in the aggregate seem sufficiently marked to support the argument for considering *croceus* and *electo* as true species.

ATTEMPTED PAIRINGS.

It was felt that the problem of specific status might be brought nearer solution if it were possible to pair *C. croceus* with *C. electo*. From the results of this experiment several possibilities presented themselves:

(*a*) With a fertile union and a subsequent fertile F_1 generation producing either intermediates or forms resembling *croceus* or *electo* in the F_2 generation the case for separation into species would be weakened.

(*b*) A fertile union producing intersexes or forms not interfertile might indicate either the extremes of a cline or separate species.

(*c*) From a union producing infertile eggs nothing definite could be indicated.

(*d*) If the insects selected for the experiment refused to pair in optimum conditions they were possibly, but not definitely, of separate species because foreign environment and food-plant might affect fertility in one potential parent.

There were practical difficulties in this experiment owing to the capricious appearance of *C. croceus* in England. In the years 1948/50 I was unable to obtain stock before early autumn. In April, 1951, an abortive attempt was made to pair *C. electo inter se* from butterflies reared in this country. Owing to cool weather the pairing cage had to be kept in a warm room by a sunny window. Growing clover and lucerne were provided. The insects fed readily on flowers and diluted honey but refused to pair, although there was considerable activity for several days in periods of sunshine. Had it been possible to maintain broods of *electo* until the autumn, when *croceus* became available, there was the problem of winter rearing in the event of successful cross pairing. At this stage Mr. Gowan Clarke offered to attempt pairings in Port Elizabeth if I could send him eggs of *croceus*. This was done in August, 1951, and a brood of *croceus* raised in South Africa was paralleled with *electo* reared from a local female. Unfortunately the result was indecisive as the *electo* males were indifferent to fresh *croceus* females. It was not possible to coincide *croceus* males with *electo* females. This experiment, therefore, had to be placed in category (*d*). However, the difficulties of transit and reversed seasons were overcome to an extent sufficient to indicate a practical method for further research, but there is still the unknown factor of a strange environment which may prove to be the most effectual barrier to pairing.

COMPARISON OF GENITALIA.

Permanent preparations were made from both sexes in *croceus* and *electo*. Material for the latter was limited in quantity but care was taken to eliminate individual differences, which however were slight. In general structure of the genitalia there is no appreciable difference between the two forms.

Characteristics of Genitalia of the Genus *Colias*.

(1) *Male.*

Eighth tergite posteriorly produced into a broad downcurved lobe overlying the genitalia proper when these are retracted. A process of the tegmen overlaps the base of the uncus, which is long. Valves short and broad; aedeagus long, strongly downcurved with long basal prong; juxta slender and V-shaped; saccus short and rounded dorsally.

(2) *Female.*

Anal lobes small, short, and broad; with club-like lateral processes: posterior apophyses slender and longer than the lobes; vestibulum weakly sclerotized, the anterior portion forming a wide, minutely papillose sac; auriculae absent; anterior apophyses short and broad; ostium wide and sclerotized; ductus rather short (relatively longer in *C. electo*); bursa spherical with a transversely elongate spinose signum (lamina dentata) placed close to the opening of the ductus.

To prevent distortion in preparation and mounting, the specimens were handled with small brushes and a ring 1 mm. in thickness was placed between slide and coverslip.

(3) *Comparison—Male.*

It was observed during low-power examinations of dried insects that the tip of the abdomen of *croceus* appeared more obtuse than that of *electo*, suggesting that the valves were set at a more acute angle in the latter. The angle was measured between the dorsal axis of the tergum of segment VII and a line drawn from the base of the false uncus to the point of attachment of the valves with the vinculum (fig. 1 (1)). It is unreliable to use the main axis of the valves as a second side because there is sometimes a small displacement during mounting; but the angle chosen, and shown by dotted lines in the figure, actually represents the chitinized tip of the abdomen and any accidental distortion would readily be apparent.

Average angles :

croceus . .	66°
electo . .	53°
pseudohecate .	60°
fieldii . .	65°

It will be seen that *electo* with the most acute angle differs considerably from *croceus* and *fieldii*, but not greatly from *pseudohecate*.

There is a slight but constant difference in the shape of the lobes at the head of the valves on the proximal boundary. The inner surface of the valve is more papillose in *croceus* (fig. 2). There is a difference in valve outline—which can be seen by reference to fig. 1. In structure the external genitalia of *electo* are somewhat more slender than in *croceus*.

The tip of the aedeagus shows a marked difference. This extremity carries a group of tooth-shaped spines in a characteristic pattern (fig. 3). The exact arrangement, and even the number of spines, varies slightly between individuals, but the group pattern remains constant. In *croceus* the spines are arranged like the head of a club. In *electo* the distal end of the aedeagus is compressed laterally with the spines arranged in line on the ventral surface. Drawings from *fieldii* and *pseudohecate* are included for comparison. It will be seen that *croceus* resembles *fieldii* and is very distinct from both *electo* and *pseudohecate*.

(4) *Comparison—Female.*

These preparations from dried material were more fragile than the male genitalia, but sufficiently clear to illustrate that *electo* was again the more slender insect, in which respect it resembled *pseudohecate*, whilst there was a general similarity between *croceus* and *fieldii* (fig. 4). Comparisons of the lamina dentata gave interesting results. On fig. 5 characteristic laminae are drawn from *croceus*, *electo*, *pseudohecate* and *fieldii*. The obvious variation is in size, which is relatively much greater than the wing spans of the respective species would suggest. These differences seem to be constant in a number of insects examined. In outline and spine pattern *croceus* and *fieldii* group together, *croceus* being larger and more complex in design, whilst *electo* and *pseudohecate* are comparable, *electo* being the smaller and simpler. *C. croceus* and *electo* differ widely.

To make clear that the laminae, which are all drawn to the same scale (× 60), are not varying merely with the size of the insect, the following ratio was calculated in each case :

Length of Tergum of Segment VII (*lateral edge*) :—
÷ *Extreme width of lamina.*
= segment/lamina ratio.

A female of each form was measured and the actual figures are set out in the table below :

Form.	(1) Wing span.	(2) Width of lamina dentata.	(3) Ratio : Wing span ÷ width of lamina dentata.	(4) Ratio Segment/lamina (See above).
croceus . .	58 mm.	1·32 mm.	44·7	1·6
electo . .	44 ,,	0·73 ,,	60·3	2·5
pseudohecate .	51 ,,	0·93 ,,	55·9	1·9
fieldii . .	54 ,,	0·93 ,,	58·0	2·3

It can be seen that in *croceus* the lamina dentata is relatively much larger in proportion to both the wing span and dimension of segment VII than is the case with *electo: pseudohecate* and *fieldii* occupy an intermediate position nearer to *electo* than to *croceus.* If ratio 3 is divided by ratio 4, a third figure is obtained giving the relationship between wing span and length of segment VII. These figures should be approximately similar as the four forms have roughly the same proportions. Actual results for ratio 3 ÷ ratio 4 are :

croceus . .	27·9	*pseudohecate* .	29·4
electo . .	24·1	*fieldii* . .	25·2

This last ratio is only intended as a check, but it is noteworthy that the rather high figure (29·4) for *pseudohecate* was given by a female with very pointed forewings.

ANDROCONIAL SCALES.

C. croceus and *C. electo*, as already mentioned, belong to a group of Coliad butterflies which have evolved a patch of scent-bearing sexual scales in the males on the upper surface of the hind wings in front of nervure 8. In addition to these two forms, all the other African subspecies are included, together with several Palaearctic, South American and one North American species, *C. meadi* (Edw.).

Members of the *hyale/erate* group were also examined. These species have no scent patches, but in the costal area of the hind wings are modified disc scales which possibly represent a stage in the evolution of the androconial scale. Longitudinal striations in disc scales run parallel throughout their length, but in androconia the striations converge to a focus at the point of attachment of the scale to the wing. Furthermore, androconia are slightly thicker and filled with a granular yellowish substance carrying the perfume.

Analysis by androconials is reliable because individual difference in scales from the same patch is very small except for the peripheral layer. Wing span of the insect makes no appreciable difference in the dimensions of the scales.

Androconials from the four forms are illustrated in fig. 6. The length and average number of striations in the widest part of the scale is given in each case. The difference between *croceus* and *electo* lies not so much in the size but in the more pointed scale of *croceus*, with 32–34 striations against 38–40 in *electo*. The count of striations is very constant for all males of any particular form and the tolerance of 2 represents the limit of variation.

I have no material of *C. hecate* but the scales of *pseudohecate* are interesting. Fig. 6 (8) from Mt. Elgon is representative of the type. It will be noted as the largest scale in the group, but has 38–40 striations, as in *electo*. Males from Njombe, T.T. (90° 20′ S. : 34° 45′ E.) have scales of the same size but rather more pointed and with 37–39 striations. However, the scales of *pseudohecate* from Mbeya, T.T., to the west of Njombe are shorter with a broad apex and 36–38 striations (fig. 6). It is possible that these are transitional either to *electo* or *hecate*. On the other hand, it may represent a racial difference, as one could hardly expect homogeneity when colonies of insects occur in isolated highlands scattered over a vast area.

The scales of *fieldii* show the same peculiarity of variation—probably for the same reason. It is a shorter scale. The three races from Tibet, Kashmir and Western China are all of the same breadth, with the same number of striations (42–44), but length and outline is distinctive for each race.

To summarize : *croceus* is distinct from the other forms ; *fieldii* and *pseudohecate* show racial variation ; *electo* and *pseudohecate* are probably more closely related than other members of the group.

MARGINAL SEXUAL SCALES.

An examination was made of the yellowish scales found loosely attached to the black borders of fresh males (fig. 7). (In addition to the four forms under discussion, *C. myrmidone* (Esp.) from Bosnia was included in the plate but is not relevant.)

These scales are very constant in shape and size. *C. electo*, *croceus* and *pseudohecate* are all widest near the apex, but *fieldii* shows a more uniform width with a sharp taper towards the tip. The number of striations is: *croceus*, 12 ; *electo*, 9 ; *pseudohecate*, 10 ; *fieldii*, 8. As with androconials, each form is distinctive. These differences in the sexual scales, relatively greater than most other distinctions described, suggest that this form of specialization in the males may still be in an active phase of evolution.

DISCUSSION.

From the foregoing observations a considerable amount of data have been presented to support the view that *C. croceus* and *C. electo* should be considered as separate species. The theory that they represent two extremes of a cline could be advanced, but it is significant that there are no forms in existence which could fairly be regarded as transitional. *C. pseudohecate* comes to mind, but now that its life-history is known it would appear to qualify for specific rank. Its affinities definitely lie towards *C. electo*, both being apparently divergent from *C. croceus*. *C. fieldii* shows some resemblance to *C. croceus*, but until its stages are known in detail it would be unwise to discuss it further. In any case, from habitat alone it could hardly occupy a position intermediate between *croceus* and *electo*. It is probable that in *C. croceus* and *C. electo* we have to-day the ends of two long branches in evolution.

SUMMARY.

The historical background for regarding *C. croceus* (Fourc.) as a subspecies of the nominotypical *C. electo* (Linn.) is reviewed briefly, together with the relationships of the other African forms and *C. fieldii* (Mén.).

A method of analysis involving detailed descriptions and examinations of all stages of *C. croceus* and *C. electo*, with comparisons of genitalia and androconial scales, is described. The allied forms, *C. electo pseudohecate* (Ber.) and *C. fieldii*, are included in these examinations.

The two forms, *C. croceus* and *C. electo*, were both reared in England and S. Africa. Pairings, which however proved abortive, were attempted between *croceus* and *electo* by Mr. Gowan Clarke in South Africa.

Distribution, imaginal characteristics, behaviour and seasonal differences are discussed in detail.

Stage by stage detailed analyses, including wintering experiments on the larvae of *C. croceus*, were undertaken, and coloured drawings prepared to

illustrate important points of difference. From this work evidence was forthcoming to support an argument for considering *C. croceus* and *C. electo* as separate species.

As the attempts to secure pairings were a failure, no support for the argument was obtained from these experiments, but a practical method for future research was indicated.

Preparations were made of the genitalia of both sexes. Several points of difference are described, notably in the aedeagus (male) and lamina dentata (female). From these examinations constant differences are again shown between *croceus* and *electo*. The genitalia of *pseudohecate* and *fieldii* are compared at the same time.

Androconial and marginal sexual scales (male) are compared. Here also constant differences are shown between the four forms, *croceus*, *electo*, *pseudohecate* and *fieldii*.

The results of this study indicate that *C. croceus* should be regarded as distinct from *C. electo*; and from both *C. pseudohecate* and *C. fieldii*. *C. electo* and *C. pseudohecate* are probably more closely related than the other members of the group. It is probable that *C. croceus* and *C. electo* represent the ends of divergent lines of evolution.

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Seitz, A., 1906–24, *Macrolepidoptera of the World*. Stuttgart. Vols. I, V.

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FIGURE 1.

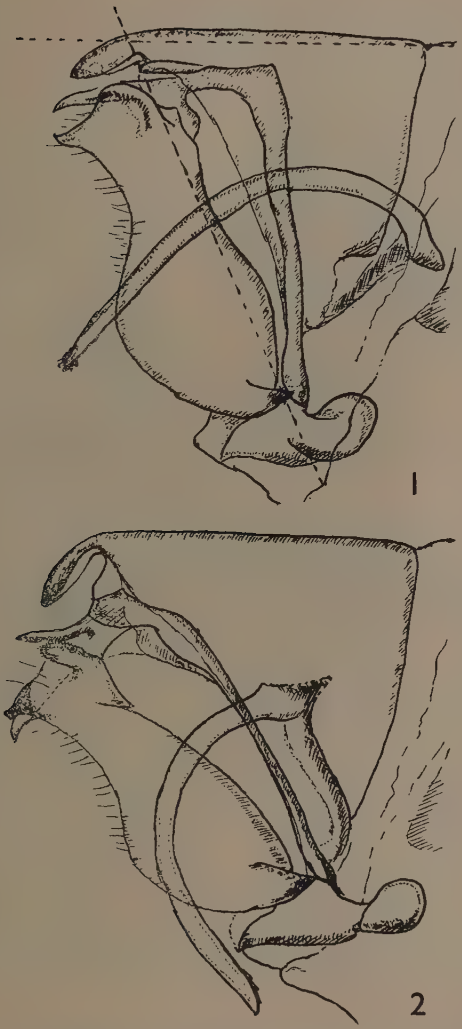


Fig. 1.—*Colias.* Male genitalia. Lateral view (× 40). (1) *C. croceus* (England); (2) *C. electo electo* (Cape Town).

FIGURE 2.

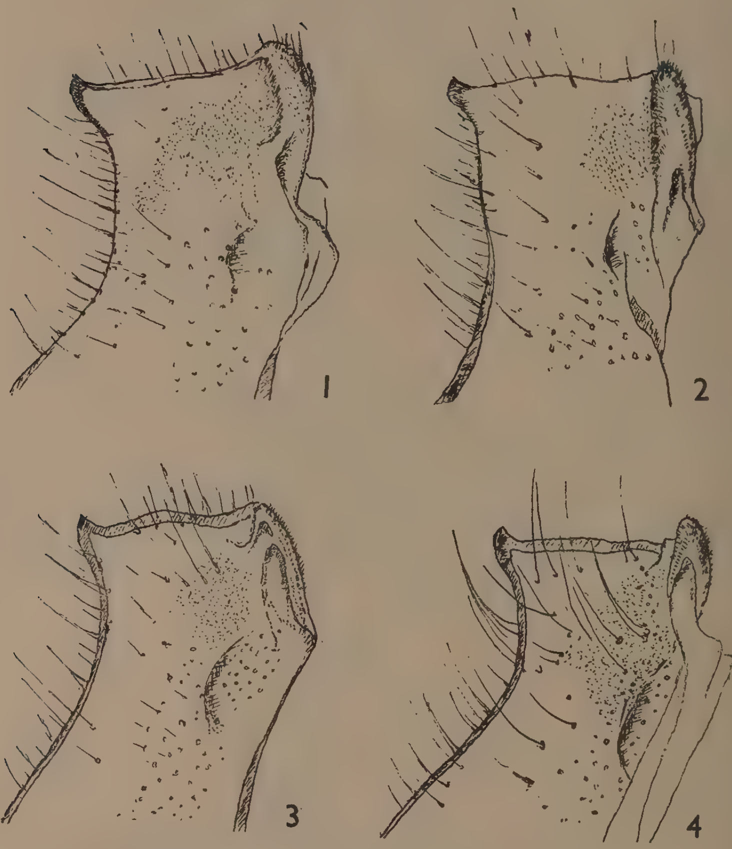


Fig. 2.—*Colias.* Dorsal portion of right valve (× 80). (1) *C. croceus* (England); (2) *C. electo electo* (Cape Town); (3) *C. fieldii* (Kashmir); (4) *C. electo pseudohecate* (Mbeya, T.T.).

FIGURE 3.

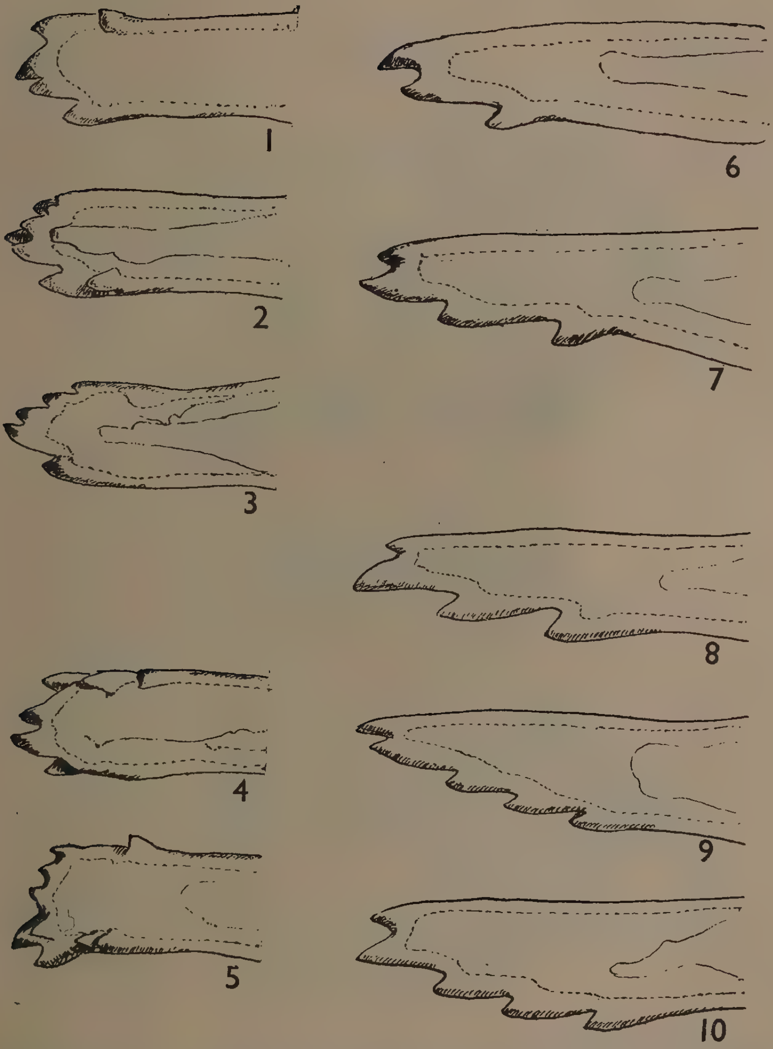


FIG. 3.—*Colias*. Male genitalia. Tip of aedeagus (× 300). (1) (2) (3) *C. croceus* (England); (4) (5) *C. fieldii* (Kashmir); (6) (7) *C. electo electo* (Cape Town); (8) (9) (10) *C. electo pseudohecate* (8, Mt. Elgon, Kenya; 9, Njombe, T.T.; 10, Mbeya, T.T.).

FIGURE 4.

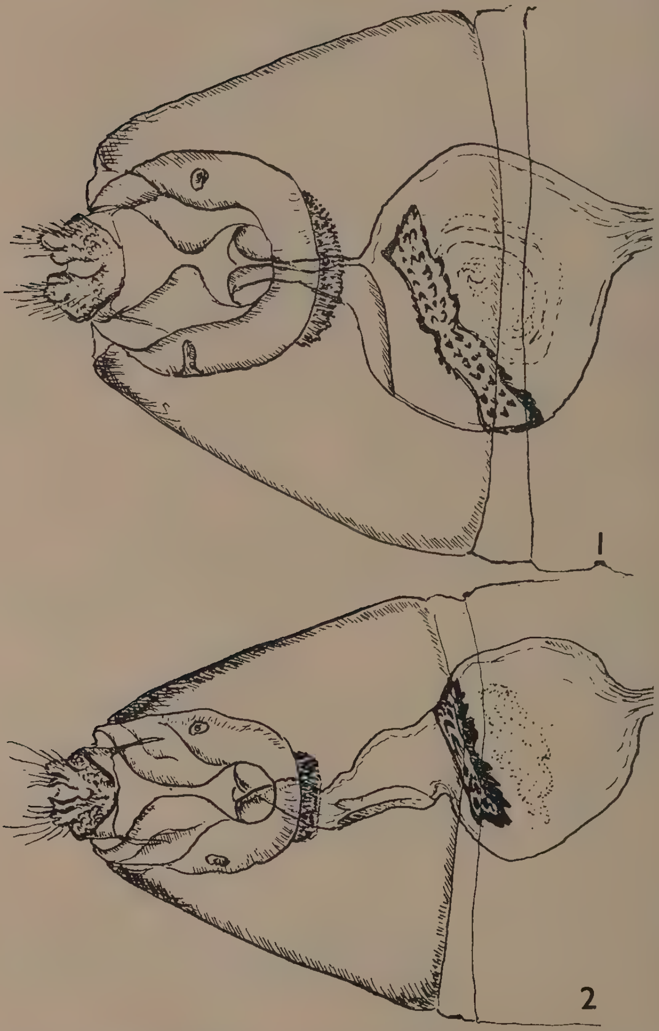


Fig. 4.—*Colias*. Female genitalia. Ventral view (× 30). (1) *C. croceus* (England); (2) *C. electo electo* (Cape Town).

FIGURE 5.

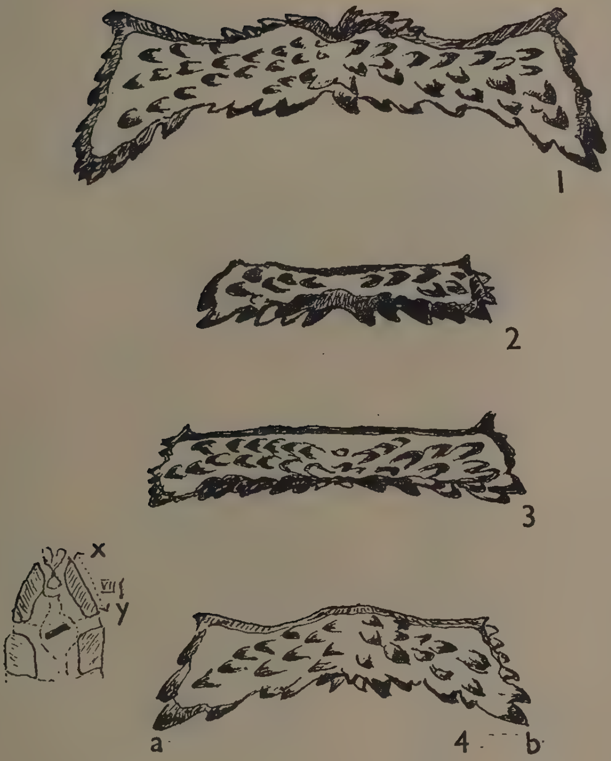


Fig. 5.—*Colias*. Female genitalia. Lamina dentata (signum) (× 60). Ratio : Length of tergum of segment VII—Lateral edge *x–y* ÷ width of signum *a–b*. (1) *C. croceus* (England), 1·6 : 1 ; (2) *C. electo electo* (Cape Town), 2·25 : 1 ; (3) *C. electo pseudohecate* (Mbeya, T.T.), 1·9 : 1 ; (4) *C. fieldii* (Kashmir), 2·3 : 1.

FIGURE 6.

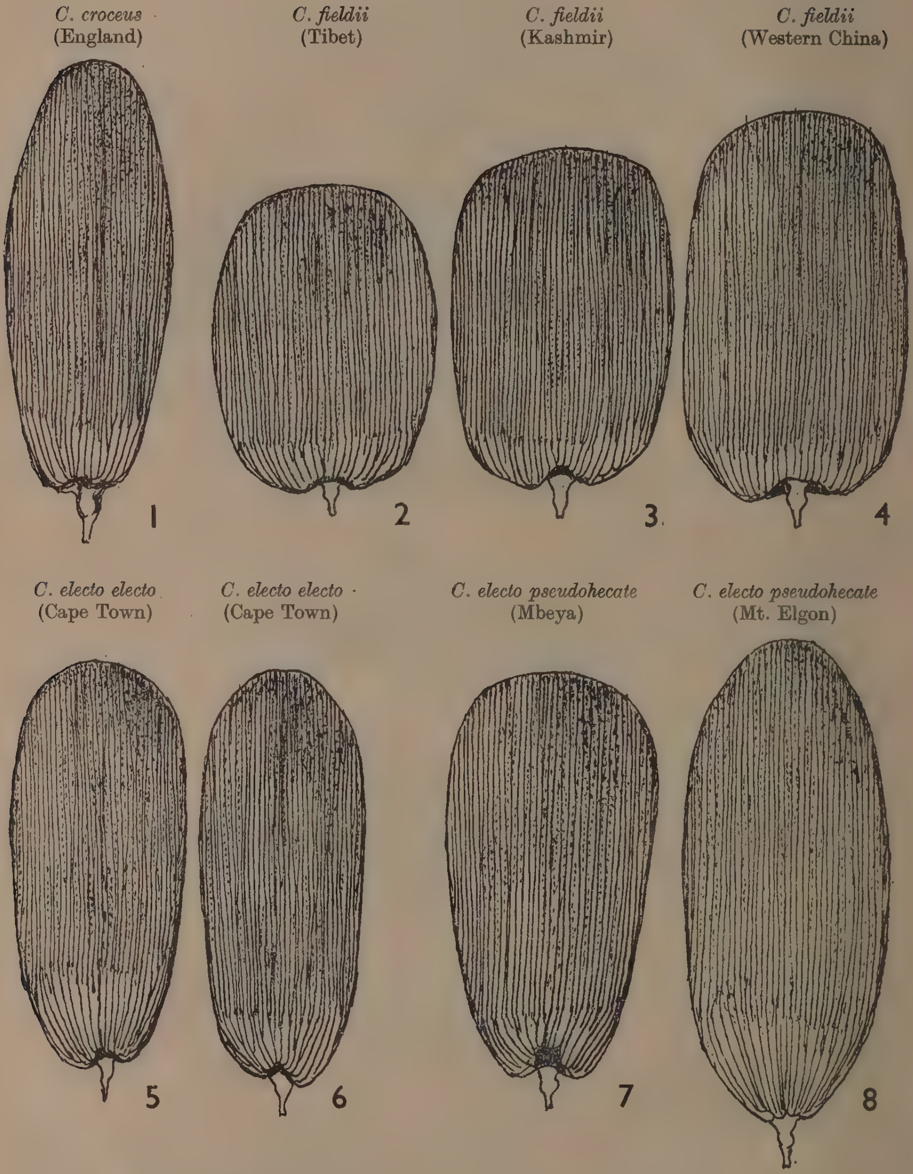

C. croceus
(England)
C. fieldii
(Tibet)
C. fieldii
(Kashmir)
C. fieldii
(Western China)
1
2
3
4
C. electo electo
(Cape Town)
C. electo electo
(Cape Town)
C. electo pseudohecate
(Mbeya)
C. electo pseudohecate
(Mt. Elgon)
5
6
7
8

Fig. 6.—*Colias.* Androconial scales (× 400). (1) *C. croceus* (England), 0·016 cm./32–34 str.; (2) *C. fieldii* (Tibet), 0·011 cm./42–44 str.; (3) *C. fieldii* (Kashmir), 0·0125 cm./42–44 str.; (4) *C. fieldii* (Western China), 0·014 cm./42–44 str.; (5) *C. electo electo* (Cape Town), 0·014 cm./38–40 str.; (6) ditto, 0·015 cm./38–40 str.; (7) *C. electo pseudohecate* (Mbeya, T.T.), 0·016 cm./36–38 str.; (8) *C. electo pseudohecate* (Mt. Elgon, Kenya), 0·018 cm./38–40 str.

FIGURE 7.

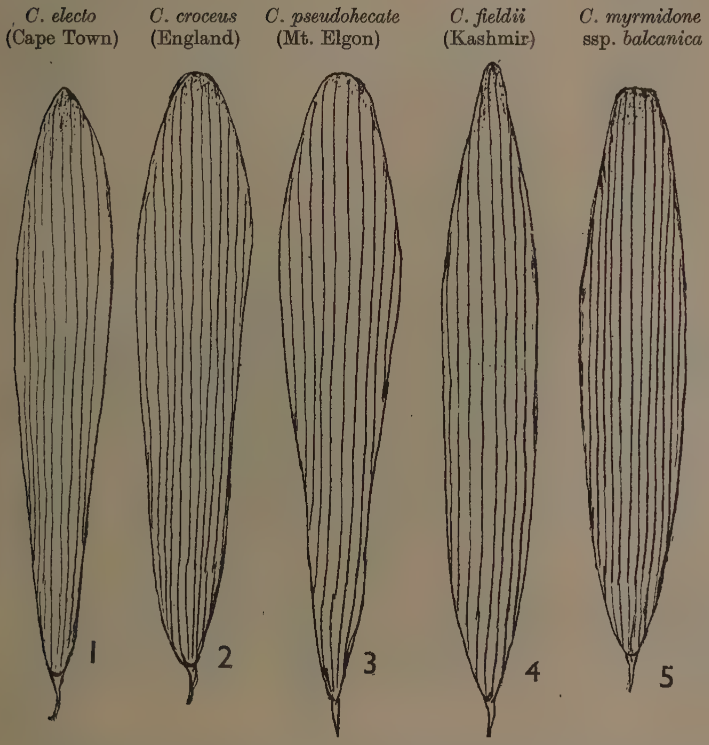

C. electo
(Cape Town)
C. croceus
(England)
C. pseudohecate
(Mt. Elgon)
C. fieldii
(Kashmir)
C. myrmidone
ssp. *balcanica*
1
2
3
4
5

FIG. 7.—*Colias*. Male sexual scales from black marginal band of fore wings (upper surface) (× 400). (1) *C. electo* (Cape Town), 0·024 cm./9 str.; (2) *C. croceus* (England), 0·023 cm./12 str.; (3) *C. pseudohecate* (Mt. Elgon, Kenya), 0·025 cm./10 str.; (4) *C. fieldii* (Kashmir), 0·026 cm./8 str.; (5) *C. myrmidone* subsp. *balcanica*, 0·022 cm./12 str.

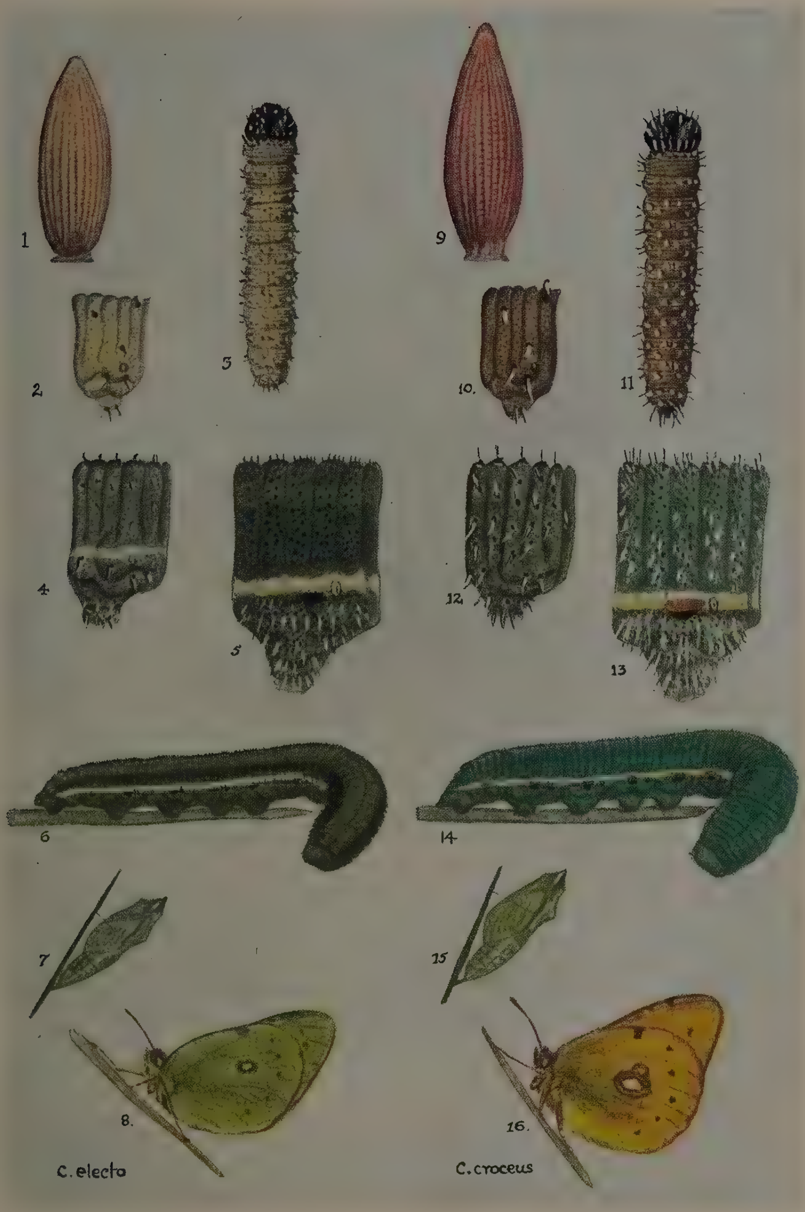
PLATE I.

Colias electo.

1. Egg (× 30).
2. 7th segment, 1st larval instar (× 40).
3. Larva on hatching (× 25).
4. 7th segment, 2nd instar (× 20).
5. 7th segment, 5th instar (× 8).
6. Adult larva (5th instar) (× 2¼).
7. Pupa (× 1).
8. Imago. Female underside (× 1).

Colias croceus.

9. Egg (× 30).
10. 7th segment, 1st larval instar (× 40).
11. Larva on hatching (× 25).
12. 7th segment, 2nd instar (× 20).
13. 7th segment, 5th instar (× 8).
14. Adult larva (5th instar) (× 2¼).
15. Pupa (× 1).
16. Imago. Female underside (× 1).


1
2
3
9
10
11
4
5
12
13
6
14
7
15
8.
16.
C. electo
C. croceus

Colias electo (Fourc.) and *Colias croceus* (L.)

F. V. L. Jarvis.

Vol. 104. Part 15*. Pp. 541–591. 14 figs. 31st December, 1953

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EFFECTS OF POPULATION DENSITY ON LARVAE OF LEPIDOPTERA.[1]

By D. B. Long, M.A., Ph.D., F.R.E.S.

Manuscript received 14th April, 1953.

(Read 7th October, 1953.)

With 2 coloured and 4 half-tone plates and 14 text-figures.

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[1] Part of thesis submitted for the degree of Ph.D. (University of London).

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Introduction.

The "phase" theory was first introduced by Uvarov in 1921 to explain certain associations of biological features in locusts. His "gregarious" phase applied to those forms having a migratory tendency, gregarious behaviour and dark coloration, whilst forms having a sedentary behaviour and a green coloration were included in his "solitary" phase. Uvarov suggested that locusts could pass from one phase to the other throughout successive generations. In subsequent studies of the conditions responsible for the production of these phases the population density was soon shown to be a major factor and a considerable amount of attention has since been devoted to the effects produced by it in locusts.

In the past breeders of caterpillars have frequently observed that their specimens were darker than those normally found in the field. On other occasions unusually dark larvae had been found in the field and these were sometimes associated with the presence of large numbers of the species. The colour and behaviour of the larvae of the Southern Army Worms of South Africa (*Laphygma exigua* Hübn. and *L. exempta* Walk.) in forming marching columns attracted the attention of Faure (1943, 1943*a*). He found that the prevailing dark colour on such columns could be produced by crowding, and the resulting larvae were more active than the light-coloured larvae which had developed under conditions of isolation. Faure considered this to be parallel with the behaviour and colour effects in locusts, and regarded the different coloured forms of the Army Worms as phases. He (1943*a*) also obtained darker larvae of the Lawn Caterpillar (*Spodoptera abyssinia* Guen.) in crowded cultures than in solitary ones, but as he could not detect any difference in the levels of activity the effects were not attributed to phases. Williams and Long (1950) reported similar colour differences attributable to the population density in the caterpillars of the British migrant Silver-Y moth (*Plusia gamma* L.).

As up to that time, with the exception of *S. abyssinia*, all the Lepidoptera and, of course, all the locusts in which a phase effect had been demonstrated were migratory species, it appeared that there may be a connection between a high larval population density and the subsequent migratory behaviour of the adults. To approach this problem the work now to be described was therefore undertaken in an endeavour to provide a better understanding of the more general effects of the population density on lepidopterous larvae, and to ascertain how far any such effects may be parallel with those occurring in locusts.

A CONSIDERATION OF THE PROBLEM AND THE TERMS USED.

In the course of the experiments various numbers of larvae have been reared in cages of similar sizes, so that the use of the term "population density" would appear to be self-explanatory. However, a closer examination of the breeding conditions shows that the term must not be interpreted in too strict a sense. The actual population density experienced by an individual larva is largely determined by the available space on the food-plant. As the larvae feed this is steadily being reduced and the population pressure increases until a fresh plant is put in the cage. Furthermore, as the larvae grow they occupy relatively more space and their capability for mutual disturbance increases. The problem is further complicated by the effects of mortality.

The term "density" therefore has been regarded as a means of describing the condition of culture associated with a given mean level of experience of the population pressure by the individual. The general term "crowding" is used to contrast conditions of culture in which several larvae were present with those of the solitary larva.

When the solitary larva has settled on a leaf it generally remains static until the leaf is either eaten or it senesces. In such circumstances, provided that adequate food is maintained, the effect of the available space on the larva is probably small, and therefore a comparison of solitary larvae reared in different sized cages would not appear to be unreasonable.

EXPERIMENTAL PROCEDURE.

1. The species used.

The nomenclature for the following list of species has been taken from Kloet and Hincks (1945). The description of a species as migrant has been based on the frequent occurrence at lightships as given by Gibbs (1941). Certain species which have been observed on less than four occasions are not regarded as migrant but may be suspected of being capable of a migratory behaviour. In the following description (Table I), therefore, these species are termed "doubtful migrants," whilst those species not listed at lightships in the above publication are termed "non-migrants", meaning that migratory behaviour has not so far been observed.

TABLE I.—*Description of species used.*

Species.	Migrant.	Generations per year.	Egg laying habit.	Normal larval population.	Predominant larval colour.	Food-plant used.
Caradrinidae (Noctuidae)						
Melanchrinae						
Diataraxia oleracea L.	No	Two or more	In tight clusters	Loosely aggregated	Variable green or brown	Brassica
Orthosia cruda Schiff	,,	One	Ditto	Ditto	Green or brownish grey	Hawthorn
O. gothica L. . .	,,	,,	,,	,,	Yellowish green	,,
O. incerta Huf. .	,,	,,	,,	,,	Green	,,
O. stabilis Schiff. .	,,	,,	,,	,,	,,	,,

TABLE I—*continued.*

Species.	Migrant.	Generations. per year.	Egg-laying habit.	Normal larval population.	Predominant larval colour.	Food-plant used.
Pieridae						
Pieris brassicae L. .	Yes	Two or more	In tight clusters.	Closely aggregated at first	Green and yellow	Brassica
Plusiidae						
Plusia gamma L. .	,,	Ditto	In loose clusters	Loosely aggregated	Green	,,
Saturnidae						
Saturnia pavonia L.	No	One	In tight clusters	Closely aggregated at first	Green and black	Hawthorn
Sphingidae						
Dilina tiliae L. .	,,	,,	Singly or in pairs	Not aggregated	Green	Elm
Laothoe populi L. .	Very doubtful	,,	Ditto	Ditto	,,	Poplar

2. The general methods used in breeding experiments.

Breeding was carried out during the spring and summer months from 1950 to 1952 under normal outside conditions in open insectaries. During the winter a small greenhouse, thermostatically heated, has been used, providing a mean temperature of 60° F. The breeding jars were exposed to extra light from a mercury-vapour and tungsten filament lamp giving both ultra-violet and visible light components. The extra light was adjusted in relation to normal daylight hours to give a minimum combined total of 16 hours light per day.

The larvae were reared in three types of breeding containers, sleeves, cages and jars.

(i) *The sleeves.*—These were made of cambric and were tied over one or more leaves of the food-plant. The sleeves were 5 in. by 3 in.

(ii) *The cages.*—These consisted of a simple wire frame covered with a large cambric sleeve. To prevent damage by wind, the frame, which was 6 by 6 by 12 in., had two prongs at one end which could be pushed into the soil when the cage stood over a 7-in. flower pot. The lower end of the cambric sleeve could then be slipped over the rim of the pot and tied down, manipulation being effected through the open upper end which could be closed with a rubber band.

(iii) *The jars.*—Short beakers from one to two litres in size were found to be generally satisfactory. In the bottom of each container was put a pad of filter-paper either dry, or slightly damped with a few spots of 25 per cent. T.C.P.[2] solution. On this was stood a 2 by 1 in. specimen tube full of water containing a stem of the food-plant mounted through a hole in the cork. In the early stages of larval development the stem had a small 5·5 cm. filter-paper collar which rested on the cork

[2] A trade product containing halogenated phenolic substances.

of the specimen tube. This collar helped to restrict the young larvae to the food-plant and helped to prevent them crawling down into the water-pot and so being drowned. As most larvae, particularly in their later stages, cannot climb glass, one or more wooden climbing sticks were put in the jar with their bases against the rim of the filter-paper pad and their tops resting against the food-plant. Larvae which then fell off the food-plant came across a climbing stick on wandering round the bottom edge of the container and so returned to the food. The tops of the jars were closed with fine muslin or cambric held down with rubber bands.

Each experiment was set up with young larvae from one batch of eggs a few hours after hatching. Generally there were two or more conditions of culture in each experiment and the larvae were distributed at random over these conditions. Care was always taken to avoid conditions leading to excessive dampness, and any wet food material was always carefully dried before being used. This, together with the use of clean apparatus and the discreet use of T.C.P. in certain later stages, enabled many cultures to be satisfactorily reared without any disastrous outbreak of disease.

A recording thermograph or a maximum/minimum thermometer was used during all experiments and a recording hair hygrograph was also sometimes used. Further an Edney paper hygrometer was used to determine the relative humidity in the cages and jars. Generally the former were 2–3 per cent. above the value outside the cage, whilst the latter were 5–10 per cent. above when not exposed to direct sunlight. If the jars were exposed to direct sunlight the relative humidity could rapidly rise to saturation associated with a rise of temperature which always tended to be slightly above the outside level.

I. EFFECTS ON MORPHOLOGY AND HISTOLOGY.

Larval Colour Observations.

1. The general effect of crowded populations.

The species previously listed were tested for a colour response by the setting up of parallel cultures of each species under solitary and crowded conditions. A review of these experiments follows in which the effects as observed in the fully-grown larvae are considered.

(i) *Diataraxia oleracea* L.—This species is normally extremely variable in colour, and on top of this range of variation the colour effect due to crowding is superimposed. Thus the colours obtained in crowded cultures are not clear cut from those occurring in solitary cultures. However, certain green, yellow or red-green larvae were produced in solitary cultures but did not occur in crowded cultures, whilst certain dark green and brown larvae were found only in the crowded cultures. From this it is apparent that there is a general colour response to a crowding condition, but the nature of this response is associated with the colour status of the individual.

(ii) *Orthosia cruda* Schiff.—The solitary larva was basically green ventrally, whilst the dorsal surface was either green or red. There was a distinct lateral stripe on either side of the body, the intervening dorsal surface carrying three fine white lines longitudinally. In the crowded culture the larvae were green ventrally but brown dorsally, and the three long white lines were more definite than in the solitary larva (Plate IA).

An interesting feature of this species was the red and green variations in the solitary larvae and the uniformity of colour throughout the larvae of the crowded culture.

(iii) *Orthosia gothica*. L—The solitary larvae were a uniformly bright green with a broad chalk white lateral stripe. Larvae from the crowded culture were a slate grey-green dorsally and the lateral stripes were a bright yellow fringed along the dorsal edge with black (Plate IB). Here again there was considerable uniformity in the black fringe and in the production of a yellow lateral stripe in the crowded culture.

(iv) *Orthosia incerta* Huf.—Some variation in the shade of the basic green colour was observed in larvae both from the solitary and the crowded cultures. However, the mid-dorsal stripe in larvae from the crowded culture was wider than that in the solitary larvae. The very fine black line adjacent and dorsal to the lateral stripe in the anterior region of the latter appeared more definite and continued along the entire length of the body of the crowded larva. Crowding also produced a general blackening extending dorsally and ventrally from either edge of the lateral stripe. This blackening, which surrounds small white spots on the dorsal surface, producing a ring effect, fades out close to the mid dorsal stripe whilst ventrally it fades out towards the feet.

(v) *Orthosia stabilis* Schiff.—The effect here was very slight, the yellowish-white flecks on the green dorsal surface of the solitary larva tending to be yellower and more definite in crowded larvae so that some sort of fine pattern appeared to exist.

(vi) *Pieris brassicae* L.—Larvae in both solitary and crowded cultures showed a variation in the stripe and fleck colour, being either white or yellow with some variation in the shade of green. There was, however, no variation attributable to the condition of the larval development.

(vii) *Plusia gamma* L.—The solitary larva is typically a whitish green with or without fine long yellowish-white lines on the dorsal surface. The crowded cultures, however, contained larvae ranging in colour from a little darker than this through an olive-green to an almost black form with distinct stripes of greenish yellow (Plate VI). Thus there was obviously a variable response reflecting basic differences in apparently similar individuals.

(viii) *Saturnia pavonia* L.—In the last instar the larva is a bright emerald green carrying six tubercular spots across each segment. These spots are frequently symmetrically incorporated to a varying degree in a black band across each segment (Plates IC and ID). The full range from the absence to maximum extent of this black band may be represented amongst larvae in both solitary and crowded cultures, the basic green colour being constant. However, it is fairly simple to define five grades for the extent of this black band (fig. 1) and, assuming these grades to represent approximately equal stages of darkening, the mean for the solitary culture was 2·7 whilst that for the crowded culture was 4·2, which was significantly different ($t = 7{\cdot}46$; $P < {\cdot}01$). From this it would appear that a colour response in *Saturnia pavonia* appears in the extent of this black band. A similar test in the fourth instar (using six grades) showed that larval crowding had already produced a significant effect ($t = 5{\cdot}97$; $P < {\cdot}01$). These results were confirmed the following year when it was necessary to introduce an extra dark grade for each of the instars.

(ix) *Dilina tiliae* L.—No readily discernible effect was noted in the colour of the crowded culture of this species.

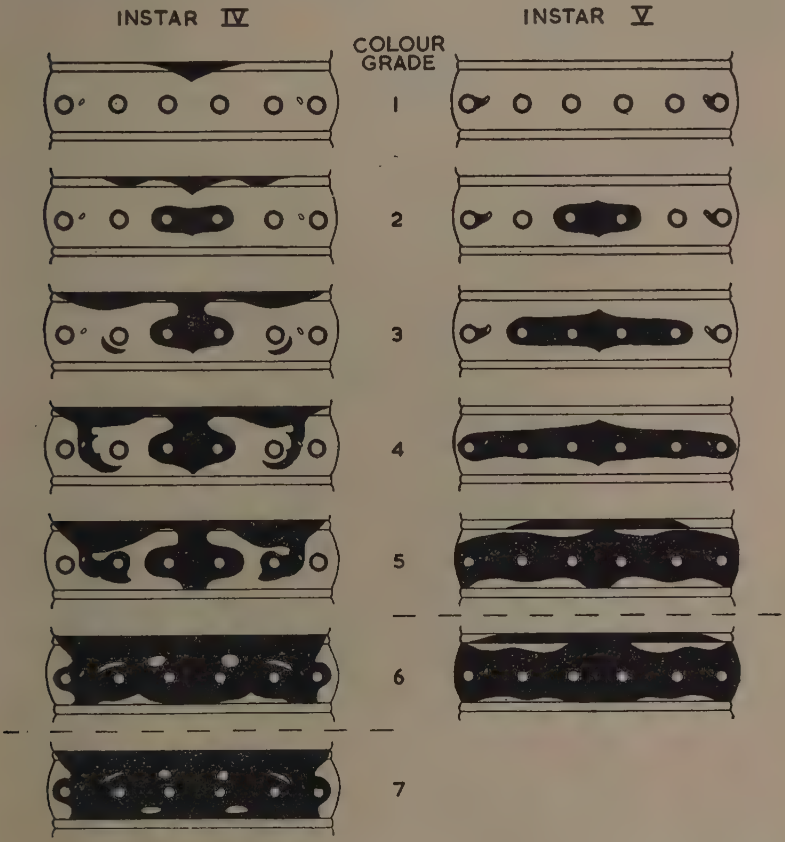


FIG. 1.—*Saturnia pavonia.* Variations in the extent of the dorsal black markings on median body segments of the larvae as graded for colour analysis.

(x) *Laothoe populi* L.—No colour effect produced by larval crowding could be discerned with this species.

From the foregoing results it can be seen that the colour response may vary in degree from species to species, ranging from *nil* in some to a very marked response in others. The non-responding larvae of *P. brassicae* follow, at least in the first part of their larval life, a fairly inactive existence in tightly packed groups; whilst the larvae of both *D. tiliae* and *L. populi* tend to follow solitary existences. Responding larvae, however, occurred in those species whose larvae tend to lead a fairly active existence within loosely adhering population. The number of species considered, however, is too small to draw any definite conclusions on this basis.

2. The histological basis of larval colour.

The colour of a caterpillar may be influenced to varying degrees by several separate components.

(i) *The intestine.*—This frequently appears a dark green (owing to contained food), and is often visible through the skin of small green caterpillars.

(ii) *The haemolymph.*—This is generally green, and may be the major colour component in green caterpillars.

(iii) *The fat body.*—Though usually white it is sometimes yellow and may be visible from the exterior.

(iv) *The hypodermis.*—This nearly always carries coloured pigments in accordance with the colour pattern of the species. Even in green caterpillars with the slightest of patterns, such as the solitary form of *Plusia gamma*, the hypodermis may still carry pigment.

(v) *The cuticle.*—Unpigmented cuticle is colourless and transparent, but with increasing pigmentation it passes through tints of straw, red brown, deep brown to practically black with increasing opacity throughout this series.

(vi) *The hairs.*—In many species these do not play much part in the general colour scheme, but in the " hairy " caterpillars the pigmentation of these hairs is a dominant feature.

A preliminary study of the basis of the coloration of three of the species was made by dissection. Since the hypodermal colours fade very rapidly during the course of dissection due to autolytic enzymatic action it was necessary to develop a modified Ringer solution to inhibit this process. The following solution proved quite satisfactory for several hours, an additional safeguard being taken by keeping it ice cold during the dissection :

Sodium chloride . . .	7·2 g.
Calcium chloride . . .	·2 g.
Potassium chloride . . .	·4 g.
Copper sulphate . . .	2·5 g.
Distilled water to make 1 litre	

The dissections were made so as to expose the entire inner surface of the dorsal area leaving the hypodermis intact. The hypodermal patterns for *Plusia gamma*, *Orthosia gothica* and *O. cruda* are shown in Plates IIA, C, D ; IIIA, C. The cuticles were subsequently cleared in 5 per cent. potassium hydroxide, when the pattern due to pigmentation of the cuticle was revealed (Plates IIB, C, D ; IIIB, D).

In the case of *Plusia gamma* (Plate IIA) the pattern, made clearly visible by a black strip placed below the caterpillar, is carried in the hypodermis, for this is absent in the corresponding cleared skin (Plate IIB). This brings out an interesting feature of pattern formation. In the cleared skin (Plate IIB) it can be clearly seen that although there is a general fairly uniform pigmentation of the cuticle, the hypodermal pattern (Plate IIA) still exists as unpigmented areas. It is as though the hypodermal pattern cast a shadow during the exposure of a photographic plate. This feature of the cuticle remaining clear above the pigmented region of the hypodermis is also shown in the longitudinal stripes of *O. cruda* (Plates IIIA, B). Since the pigmentation of the hypodermis is an intracellular function whilst that of the cuticle almost certainly involves diffusion, it seems probable that the pigment-carrying hypodermal cells are maintaining some form of inhibiting potential in the overlying cuticle.

These dissections showed that in the species considered the hypodermis was responsible for the actual colour differences between solitary and crowded larvae, whilst the darkening of crowded larvae was due to pigmentation of the cuticle. The extreme effect of this darkening is well shown in *P. gamma* (Plate IVA) and *O. cruda* (Plates III B,D).

A further histological study of the above material was made by serial section. This showed that the groups of pigment-carrying hypodermal cells such as in the spiracular and dorsal stripes were often considerably larger and different in nature from the remainder (Plates IVB, C, D). Even non-stripe cells are enlarged when carrying pigment, as shown by general hypodermal cells of the red form of solitary *O. cruda* larvae (Plate IVB), which may be contrasted with the green form (Plate IVC) where pigment-carrying cells are virtually limited to the stripes.

The morphology of the cuticle surface was peculiar to each of the species studied. In *P. gamma* the cuticle is intensely spinose, the spines being relatively small and buttressed (Plates VA, B). The cuticle of *O. gothica* is fairly uniformly papillose, whilst in *O. cruda* it is irregularly granulate and variably beset with acuminate spines.

The pigmentation of the cuticle appears to be a surface phenomenon, the area of which may terminate abruptly or end in a gradation. Such gradations show that in *P. gamma* the colourless spines darken progressively from the top towards the base (Plate VB). This would support the suggestion (above) that lack of pigmentation is due to a process of inhibition or destruction originating from beneath in the hypodermal cells. In the dark areas the spines appear to be more numerous. In *O. cruda* the spines darken progressively in a somewhat similar manner and this is accompanied by a darkening of the granules (Plate VC). These darkened granules seem to be most numerous in the darkest regions, where the remainder of the superficial layers of the cuticle still appears to be clear. The pigmentation of the cuticle of *O. gothica* differs in that the darkening affects both the papillae and the surface layer of the cuticle (Plate VD).

3. The development of colour within solitary cultures.

A general description of the colours of the solitary larvae has already been given. With the construction of a colour scale described in the next paragraph a closer examination was possible of the solitary cultures of *Plusia gamma*. This showed that a small range of variation existed from whitish green forms with no clear discernible pattern to medium green forms with a distinct pattern covering colour groups 1–3. A large proportion of each culture, however, always occurred in group 1. A typical colour composition for a solitary culture is given in fig. 4B.

4. The development of colour within crowded cultures.

Out of all the species which showed a colour response to crowding, *Plusia gamma* presented most clearly a range of variation in the degree of response. Whereas the solitary cultures of *Plusia gamma* showed only a small range of colour variation and were typically light, within the crowded cultures could be found a wide range of variation from light forms showing little or no response to very dark forms. From the complete range of colour forms shown by this species it was possible to construct a colour scale in the form of hand-coloured drawings. The full colour scale finally represented 14 successive grades of darkening by approximately equal stages. In all later work on this species this scale was used as the standard reference. For much of the experimental work and calculations this colour scale was grouped to illustrate five major colour ranges (Plate VI).

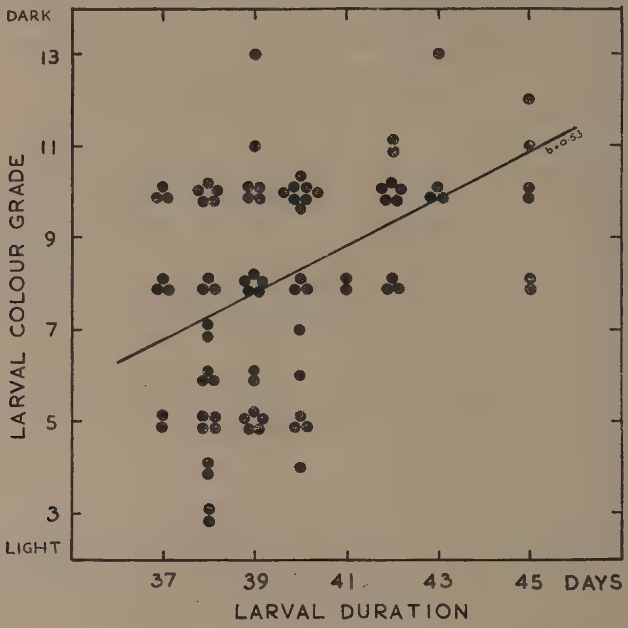


Fig. 2.—Scatter diagram and regression line showing relation of larval duration and larval colour within the first 82 per cent. of a crowded culture to pupate.

The colour grade of a larva was determined against this scale when the larvae reached a selected point in the instar development, as determined by the width of the first segment being slightly greater than the head width, with the second segment bearing a similar proportion to the first segment. The selection of this point which represents approximately the stage of development in the middle of the instar will be discussed later.

The head-capsule shows a range of coloration which can be correlated with the body colour, but the head colour is more variable and the maximum darkening is associated with colour grade 8.

This variation of response in the crowded cultures of *Plusia gamma* was associated with another most interesting feature. This was that the larvae showing the least degree of response developed the most rapidly and pupated first, whilst the darkest larvae were nearly the last to pupate (fig. 2). *S. pavonia* shows a range of forms in both crowded and solitary cultures, but in neither does it show any similar difference in rates of development.

5. Population density and the degree of response.

It can be readily appreciated that until we know more about the operating factors in a crowded culture, in making even the simplest of approaches in terms of population density, we cannot be sure that the number of cc. per larva means the same thing for populations of different sizes. Do 100 larvae in a volume of 1 litre present similar conditions to 200 larvae in 2 litres ? Should the response depend on contact between two larvae, then a greater level of response would be associated with the larger culture where a greater opportunity exists for such contacts. However, some preliminary considerations on the value of term " density " as applied to populations of larvae have already been given (page 545), so that it can be seen that from a practical standpoint it would be difficult to separate experimentally the effects of population density from those of population number, and this has not been attempted. The results of experiments carried out in breeding at various densities therefore must always be viewed in the light of the conditions of the experiment.

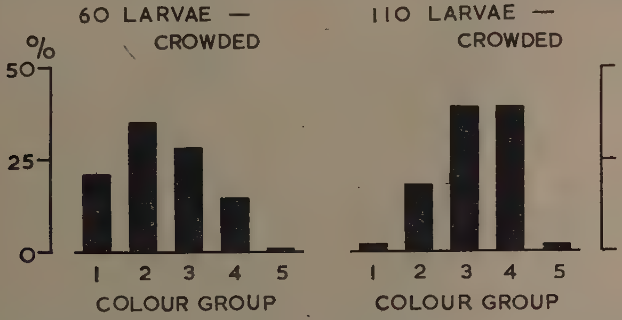


FIG. 3.—Histograms showing the effect of increasing population density on the percentage colour composition (for values of colour groups see Plate VI).

Generally a rise in population density is associated in *Plusia gamma* with an increased darkening of the mean colour of the culture (fig. 3). Naturally the question must arise as to the minimum number required to produce a response. Two experiments were set up to give 6 sets of each of the densities from 1 to 6 larvae per container but, owing to the onset of winter in one experiment and an excessively high rate of mortality in the other, they had to be abandoned and are now being repeated. Further, it is of interest to know if the response to population density follows a simple arithmetic series or a geometric series of densities. An experiment was set up (from a stock of eggs obtained from the Insecticides Department of Rothamsted), providing 27 cultures of 3 larvae per container, 9 cultures of 9 larvae, 3 cultures of 27 larvae and 1 culture of 81 larvae with 50 solitary controls. The experiment unfortunately collapsed due to the accidental destruction of the food-plant reserves, for under conditions of relative food shortage the larvae indulge freely in cannibalism, which reduces the size of large cultures very rapidly. However, the solitary cultures and the cultures of 3 larvae were successfully reared. Although the solitary larvae were still typically light, the groups of three showed larvae approaching both extremes of the complete colour range and giving therefore a rather unusual colour distribution. Thus, although the unusual nature and degree of the response may possibly be attributed to the use of a different stock, the experiment does show that cultures with densities as low as 3 larvae per container can produce marked colour responses. In other experiments where two larvae have been bred together colour responses in ranges 2 and 3 have sometimes been obtained though, from the variable nature of the darkening response in general, the numbers of such cases have been too small to obtain a significant result.

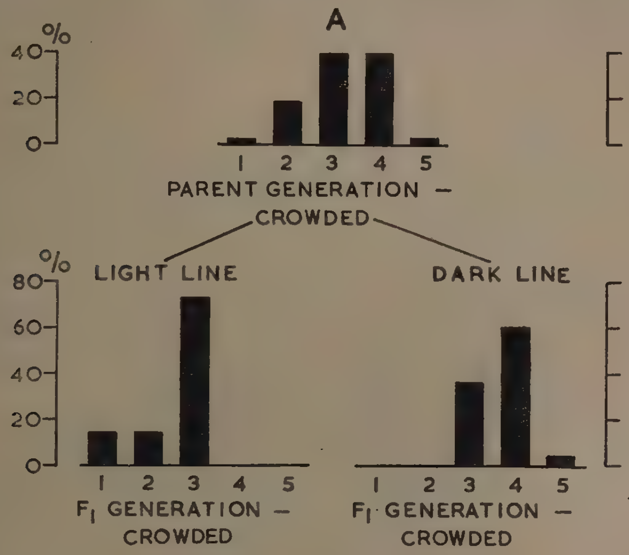
6. The effect of the genetic strain in *Plusia gamma.*

The fact that light-coloured larvae always occurred in crowded cultures even at high densities seemed to indicate that at least two genetic strains might be involved. One such strain could carry the potentiality for producing dark pigmented forms whilst the other carried little ability for pigmentation. This point was tested experimentally in 1951 by setting up two selected lines from a crowded culture. In one line adults developing from dark larvae were allowed to breed, whilst in the other line the adults came from light larvae. From these two lines parallel cultures of crowded and solitary larvae were set up. The results of this selection as appearing in the colour composition of the F_1 generation are expressed in fig. 4A. It can be seen that in the parent generation colour groups 1 to 5 are all represented. In the F_1 generation of the light line the light to medium colours only are represented in groups 1 to 3, whilst in the dark line it is the darker colours in groups 3 5 that are produced.

No significant effects, however, appeared in the colour composition of the F_1 generation in the solitary cultures of the dark line (fig. 4B). Most of the larvae in the solitary cultures of the light line failed to develop beyond the third instar so that no results were obtained. From these results it does look as though genetic strains do exist, and it may be possible to isolate them.

It has already been stated that experiments were set up at random from one batch of eggs to eliminate as far as possible the effect of any genetically controlled tendencies. This permits parallel cultures in a given experiment to be compared. This technique, however, cannot obviate the effect of a continual process of selection that must be going on throughout successive generations; for, quite apart from deliberate selection, forms least suited to the conditions of breeding will tend to have the lowest rate of survival. This means that unless the culture is breeding genetically true to type a degree of disparity can occur between two successive generations. Further, this disparity may increase between each successive generation and that of the original parents.

In the case of the light and dark selected lines it was highly improbable that either of the F_1 generations were genetically pure for the selected factors.



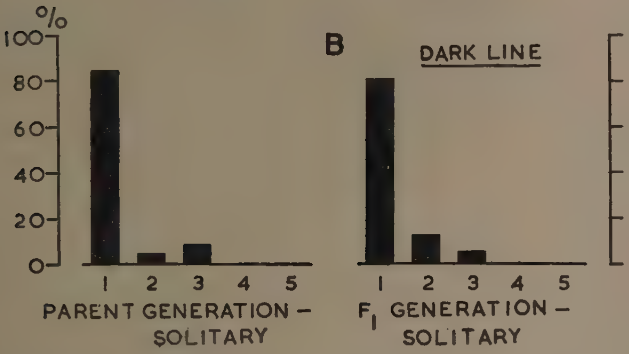


Fig. 4a.—The effect on the colour composition of the F_1 generation of selective breeding from light and from dark larvae in a crowded culture.

Fig. 4b.—Shows the lack of effect on the colour composition of the F_1 generation under solitary conditions by the dark larval colour selection in fig. 4a.

It was proposed therefore to continue the selected lines whilst cross-breeding the remainder in order to maintain a stock resembling as near as possible the original. Unfortunately the F_2 generation of the light line failed completely, and so did the attempts at cross-breeding. As a result of this, selective breeding of the dark line was stopped and as much as possible of the later breeding was carried out from medium-coloured forms. However it was seen that in later crowded cultures the light forms, as typified by colour group 1, are virtually absent and the mean colours of the entire cultures are darker. With the absence of the light forms the established order of colour development within the crowds also vanished along with other features discussed later. However, simple breeding experiments with new wild stock in the late summer of 1952 confirmed the trends shown in the experiments of 1950 and the spring of 1951.

7. The general development of colour throughout larval life of *Plusia gamma*.

In the first few instars the larvae of both solitary and crowded cultures are varying shades of leaf green depending on the gut contents. As the end of each instar is approached the larvae change to a greenish yellow prior to the swelling up of the new head capsule. Some larvae from both cultures may be covered with a variable number of small black tubercular spots. By the 4th instar the pattern begins to appear. At this stage too a larger colour range is to be found in the crowded culture with the appearance of darker larvae. From then on the population darkens with each instar (fig. 5A).

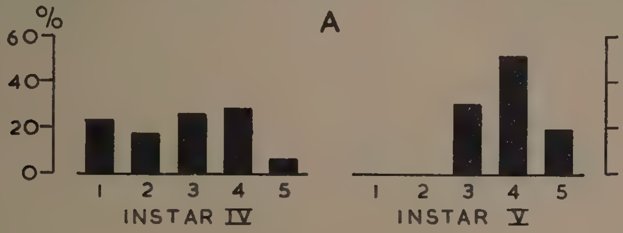
During the last 2 instars the colour development can be clearly seen, and also the different courses followed in the solitary and crowded cultures. In the solitary cultures the newly moulted larvae may show a fair range of variation, but as the instar proceeds they generally fade to a more uniform light coloration (fig. 5B). Just as in the early instars the larvae become yellowish prior to ecdysis, but during the moult some pigment is laid down. As a result a larva which was colour grade 2 in the last but one instar may appear in the next as grade 6 or darker before fading to grade 1 or 2. Finally with the approach of the pre-pupal stage the larvae change their colour in quite a different manner and are not represented on the colour scale.

In the case of the crowded cultures the caterpillars appear darkest immediately after shedding their old skin. As they grow within the instar they become progressively lighter and finally turn yellowish just prior to the next moult. At the beginning of the last instar the new larvae show the darkest range of colour that will be attained ; then, as before, they become lighter with growth and lose their general pattern of pigmentation just before the prepupal stage.

This phenomena of the gradual change of colour throughout growth within each instar necessitated a system of fixing the point of development at which the colour grade determination should be made. In order to include as much of the effect of the condition of culture on the last instar it should be as late as possible, but at the same time the period of pigment dissolution must be precluded. For these reasons a point near the middle of the instar appeared to be the most suitable time for the determination, details of which have already been given (pages 552–553).

As can be seen the feature of colour-fading throughout the instar applies to both the solitary and crowded cultures, although the basis of their final colours have been shown to be histologically different. Naturally a certain amount of the fading can be attributed to the stretching of the larval skin with growth, but the problem still remains as to whether fading acts differentially on the pigments with different conditions of culture.

Since colour differences between solitary and crowded cultures do not begin to appear till about the 4th instar, an experiment was set up to determine the effects of the population density during instars I–III as compared with its effect during the remaining instars. Five lines of culture of *P. gamma* were set up for comparison :



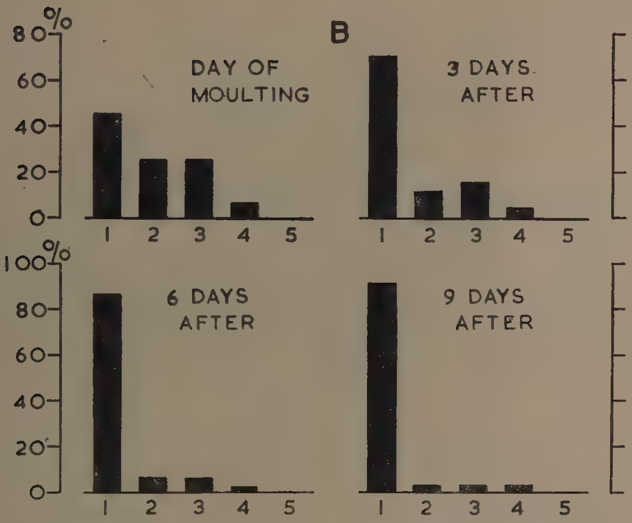


Fig. 5a.—The general darkening of the colour composition of a crowded culture on changing from instar IV to instar V.

Fig. 5b.—The change with time of the colour composition of solitary cultures in the last instar.

Line 1 : Fifty solitary cultures.

Line 2 : Fifty solitary cultures for combination into one crowded culture when 50 per cent. of the individuals have reached instar IV.

Line 3 : Fifty solitary cultures for combination into one crowded culture simultaneously with the division of the crowded culture in line 4 below.

Line 4 : Crowded culture of 50 larvae for division into solitary cultures when 50 per cent. have reached instar IV.

Line 5 : Crowded control culture of 50 larvae.

In this experiment, for simplicity, only the colour change from one instar to the next is considered. Thus colour changes from instar IV to instar V and from instar V to instar VI may be related to the period of changed condition of population density. The results of the experiment are given in Table II.

TABLE II.—*Incidence of newly moulted larvae.*

Line.	Instar.	Instar mean duration in days.	Days since change of conditions.	Colour groups. 1.	2.	3.	4.	5.	Group mean.	
1	—								1·0	
2	IV	6·0								
	V	7·0	2	4	1	2	.	.	1·7	
			4	1	2	2	4	.	3·0	
			6	.	.	2	4	.	3·7	
			8	.	.	2	1	1	3·8	
	VI		6	.	.	2	2	1	3·8	
			8	.	.					
			10	.	.	1	7	2	4·1	
			12	.	.	.	1	2	4·7	
3	IV	5·9								
	V	6·0	4	.	.	1	.	.	3·0	
			6	.	.	.	.	1	5·0	
			8	.	.	2	4	.	3·7	3·9
			10	.	.	.	7	.	4·0	
			12	.	.	.	2	1	3·8	
			14	.	.	2	1	1	3·8	
			16	.	1	.	3	3	4·3	
	VI		8	.	.	.	1	.	4·0	4·5
			10	.	.	.	.	2	5·0	
			12	.	.	.	1	.	4·0	
			14	.	.	.	1	2	4·7	
			16	.	.	.	3	1	4·3	
			18	.	.	.	4	2	4·3	
			20	.	.	.	2	3	4·6	
4	IV	6·0								
	V	7·0	4	.	1	3	3	2	3·7	
			6	2	2	2	1	.	2·3	
			8	5	3	.	.	.	1·2	
			10	2	.	.	.	.	1·0	
			12	.	2	.	.	.	2·0	
	VI		6	1	.	.	.	.	1·0	
			8	.	.	.	.	.	.	
			10	3	.	1	.	.	1·5	
			12	6	.	.	.	.	1·0	
			14	8	1	.	.	.	1·1	
			16	1	2	.	.	.	1·7	
			18	1	.	.	.	.	1·0	
			20	3	.	.	.	.	1·0	
			22	1	.	.	.	.	1·0	

TABLE II—*continued.*

Line.	Instar.	Instar mean duration in days.	Days since change of conditions.	Colour groups. 1.	2.	3.	4.	5.	Group mean.	
5	IV	5·4								
	V	6·6	2*	.	.	.	2	2	4·5	4·3
			4	.	.	.	2	2	4·5	
			6	.	.	1	4	3	4·3	
			8	.	.	.	3	2	4·4	
			10	.	.	.	3	.	4·0	
			12	.	.	.	2	1	4·3	
	VI		4	.	.	.	.	1		4·6
			6	.	.	.	.	4		
			8	.	.	.	3	1		
			10	.	.	.	6	5		
			12	.	.	.	3	1		
			14	.	.	.	.	4		
			16	.	.	.	.	2		
			18	.	.	.	.	1		
			20	.	.	.	.	1		

* As determined by line 4.

From breeding lines 2 and 3 in Table II it can seen that darkening due to crowding is very rapid. Thus larvae which had been crowded for the whole of instar IV and moulting into instar V six to eight days after the change of conditions had nearly attained a colour-group mean of 4, whilst larvae moulting at four days in line 2 show that most of this effect was produced by exposure to crowding in the last half to two-thirds of the previous instar Larvae moulting into instar VI in lines 2 and 3 not only darken at a similar rate, but show by increased darkening with exposure to crowding over more than one instar that the effect is cumulative.

Line 4 shows by comparison with line 5 that a reduction of colour intensity is occurring in crowded larvae which have been isolated for the last three to four days in instar IV. The group mean of 2·3 for next larvae to moult infers a residual colour effect of crowding in instars I–III. In instar V of line 5 the group mean is higher than that of lines 2 and 3, though the means of all three lines for instar VI agree well. This implies that crowding in the early instars can affect the degree of darkening of the culture right up to instar VI.

The results of this experiment show that the potential mean colour of a crowded culture is being influenced by the population density in the early instars long before such effects become visible. The power to respond is not affected by the condition of culture during this period, as larvae subjected to crowding later may ultimately still attain the same level of colour darkening. The relationship between the larval colour and the period of changed conditions for this experiment is expressed in fig. 6, which shows how crucial is the period just prior to ecdysis when presumably the hypodermis is undergoing a renewed period of activity. At least in the case of larvae which have been crowded, a change to a solitary condition during this period has little effect on the colour

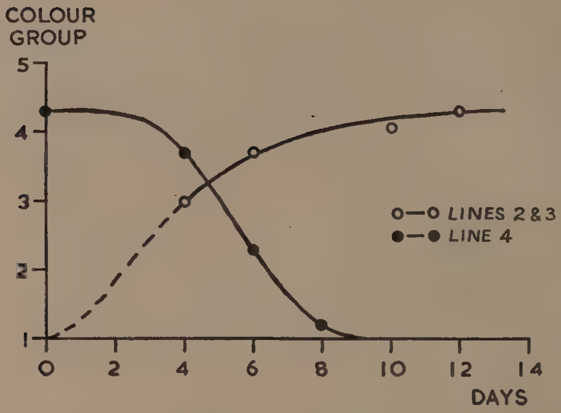


Fig. 6.—Changes with time of larval colour after reversing the conditions of culture (for details see text).

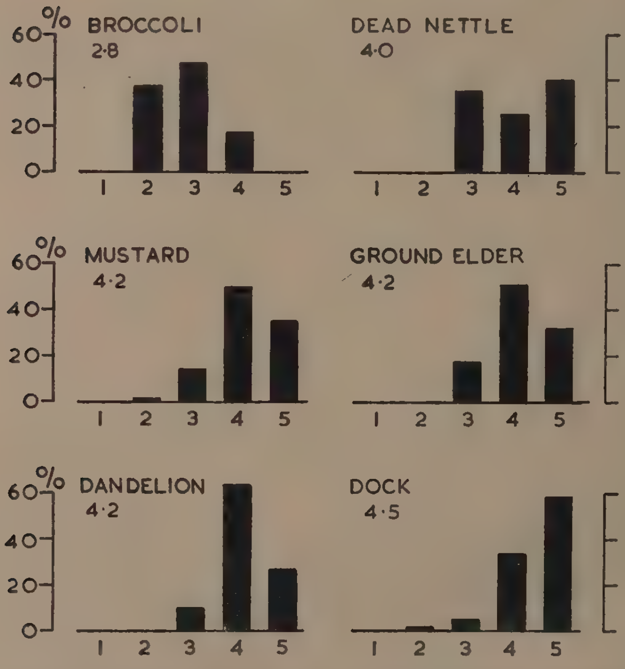


Fig. 7.—The effect of different food-plants on the colour composition of parallel crowded cultures. The appropriate colour group mean is given below each plant name.

of the next instar, whereas a change occurring in the early part of the instar leads to a marked falling off of the ensuing colour. With larvae which have been freshly crowded the colour build-up is very rapid, and though more points are needed to fix the shape of the early part of the curve it does seem probable that darkening can take place in the pre-moulting period.

8. The effect of the food-plant (*Plusia gamma*).

In order to assess the relative importance of the population density in determining the mean colour of a population in the field it is naturally necessary to know what other factors can influence the colour. In the larval life the food-plant must be considered a dominant feature. The larvae of *Plusia gamma* will feed on a wide variety of low-growing plants. Accordingly parallel crowded cultures were set up on Broccoli, Dandelion, Ground Elder, Dead Nettle, Dock and on Agricultural Mustard. The results clearly showed that the food-plant can affect the colour composition and the mean colour; Broccoli resulting in the lightest with a group mean of 2·8 whilst Dock produced the darkest with a mean of 4·5. The mean colours from the other plants were closely placed with means of 4–4·2, and so were nearer to the dark extreme. The results are illustrated in fig. 7, which shows a normal colour distribution for each food-plant with the exception of Dead Nettle. From the colour compositions it appeared that our previous choice of Agricultural Mustard for the standard food-plant was fortunately placed. Since Dock resulted in the darkest larvae this plant was selected along with Dandelion and Mustard for the food-plants for three parallel solitary cultures. This control experiment showed no colour differences between the solitary larvae on these plants and that the larvae were typically light.

9. The specificity of the crowding response (*Plusia gamma*).

In the foregoing experiments the reaction of larvae to other members of their own species has been considered. It still remains to be ascertained if the response is species specific or if the larvae will react to members of other species. Although some preliminary experiments have been carried out in this direction certain technical difficulties must be considered. The first is that it is necessary to breed several crowded cultures of larvae of one or more species, and that these must be synchronised with the development of the solitary larvae of the species to be tested. Further, all the larvae must be able to feed on the same food-plant. Finally if *Plusia gamma* is used for the test species, a negative result with only a few cultures does not necessarily mean the response is specific as the tested larvae may have been of a light strain.

In an early experiment set-up to approach this problem one *Plusia gamma* larva was introduced into each of three crowded cultures of *Pieris brassicae* feeding on cabbage. The result in each case was negative, which is not surprising from the different type of behaviour exhibited by *P. brassicae* and also from the nature of the food-plant. A later experiment was attempted introducing *P. gamma* larvae into crowded cultures of *Diataraxia oleracea* feeding on Agricultural Mustard. In this case the habits of the two species are much more closely allied. The result was still indecisive as both light and medium coloured larvae were produced and the number was too small for statistical analysis. Although this question of specificity is naturally of interest it does seem unlikely that it can ever play much part in the field.

10. Larval senses and colour response.

References to colour changes in response to the colour of larval background have already been made elsewhere (Long, 1952) and much of the research done on that phenomenon shows that the sense of sight is involved. Colour changes in response to the larval population density, from their very nature and from their speed of action, seem to indicate that the sensory system is involved, in which case the pigment production could be an effect of a neuro-hormonal reaction. Should a simple sense be identified with the response it may prove a valuable guide to the understanding of the mechanics of the response. A preliminary approach therefore has been made to the senses of sight, smell and contact. One of two parallel crowded cultures of *P. gamma* larvae was reared in total darkness whilst the other served as a control in ordinary daylight. The resulting colour composition of these cultures showed a mean colour group of 4·8 for the culture in darkness against a mean of 3·9 for the daylight control. This certainly seems to indicate that the sense of sight is not involved, for even more dark forms were produced when the sense is not operating. A further experiment was set up in which solitary larvae were reared in isolation in glass tubes or small muslin cages mounted in the centres of large crowded cultures. The arrangement was such that the larvae in the glass tubes experienced vision of their crowded surroundings but were otherwise isolated from them, having no physical contact with other larvae, and an independent air supply via air ducts which were led clear of the crowded culture. Those larvae in the muslin cages could not experience vision of the surrounding crowd, but could be subject to the diffusion of any gases associated with the crowd and also to a limited degree of contact through the cambric walls of the cage. A set of solitary control cultures were also reared.

The larvae which had free vision resembled their solitary controls, and in this support the indication above that the sense of sight in itself does not play the vital part. A proportion of the larvae which had been bred in the cages, however, showed typical dark coloration, and so indicate that senses of contact or smell or both conjointly may be involved in the colour response. The results of this experiment have not yet been subjected to the test of repetition, and even if a similar result is obtained caution must be taken in interpreting the results until the conditions prevailing in the experiment have been more fully studied.

LARVAL SIZE.

An analysis of the size of male and female larvae as represented by the weights of their freshly formed pupae showed, over the course of the experiments, that with *Plusia gamma* the female is slightly lighter, being 96 per cent. of the male weight.

A further analysis of the weights of parallel solitary and crowded cultures when corrected for the sex composition showed mean weights as follows :—

Solitary cultures, 276·7 mg.
Crowded cultures, 274·3 mg.

Although the difference is only 2·4 mg. (less than 1 per cent.), there is good reason to believe that this trend is correctly represented. The significance of this point will be discussed later (see page 568).

No correlation has been found to exist between the head capsule width and the larval colour.

II. EFFECTS ON THE PHYSIOLOGY.

Population Density and Larval Duration.

When breeding parallel solitary and crowded cultures of larvae we frequently observed that development of the crowded culture was more rapid than that of the solitary cultures. In nearly every case where the larval durations were compared this proved to be the case. The mean duration of the crowd was generally from 70 to 90 per cent. of the mean duration of the solitary cultures.

The mean duration of 40 solitary larvae of *P. brassicae* was 37·6 days, whilst two crowded cultures of about 60 larvae in each had means of 30·5 and 31·2 days, equivalent to 81 and 83 per cent. respectively of the solitary duration. In *D. oleracea* the duration of the crowded culture was less than 70 per cent. of the solitary duration. Similar effects have also been obtained in *P gamma* where the crowded culture complete their larval life in about 75 to 80 per cent. of the time taken by the solitaries. Only a slight effect was observed in *S. pavonia,* the duration of the crowd being 92 per cent. of that of the solitaries.

The effect of various densities in terms of the subsequent duration has not yet been directly determined, but in *P. gamma* some further observations have been made from an experiment in which parallel cultures of 1 crowd of 50 larvae 6 crowds of 12 larvae and 50 solitary controls were set up. As occasional mortality occurred in the crowds of 12 larvae the number was maintained by splitting up two of the crowds. In the crowd of 50 and the 50 solitaries there was a steady reduction in number throughout the experiment. The state of development after 28 days is summarised in Table III.

Table III.—*The percentage instar composition of* P. gamma *cultures after* 28 *days of larval life.*

Condition of culture.	No. of larvae.	I.	II.	III.	IV.	V.	Mean instar.
Solitary	37	.	.	14	32	54	4·41
Crowds of 12	35	.	.	.	17	83	4·83
Crowded	31	.	.	.	10	90	4·91

From these results it can be seen that the development of a density of 12 was nearly as rapid as a crowd of probably more than three times this density. When comparing the mean instars the crowds of 12 larvae achieved 84 per cent. of the advance of the bigger crowd over the solitaries. Thus it appears that the relationship between the population density and the shortening of the larval duration may not be expected to follow an arithmetic series, and also that an effect may be obtained at relatively low densities.

As a culture of young larvae developed, the period during which moulting was taking place tended to increase for each successive instar as the individual moults became more and more out of step. This tendency appeared to be greater in solitary cultures than in crowded ones, so that the period during which pupation was taking place was generally greater in the former. Frequently there were a few larvae in a solitary culture which developed extremely slowly either pupating some weeks after the others or failing to reach this stage at all. These larvae have not been included in the larval duration calculations given above; thus the estimates given for the differences between solitary and crowded cultures are on the conservative side.

The Number of Instars.

Development throughout larval life has been largely considered in terms of the instar, determination of which has been based on measurements of the width of the head capsule. The head-width is in point of fact extremely variable, being more properly related to the weight of the larva at the end of the preceding instar. This, with other observations, has led many authors such as Beck (1950) to conclude that Dyar's progression factors have no fundamental basis and, though later reference is made to Dyar's factors, these considerations have to be borne in mind. However, by a system of repeated measurement at two- to three-day intervals over the course of larval duration, it was possible to determine the instar succession in solitary cultures of *P. gamma*. The frequency of the various head-widths of a typical solitary culture is illustrated in fig. 8A. An analysis of the individual head-width changes of the culture showed that there were two distinct series (Table IV).

Table IV.—*Successive mean head-widths and progression factors in* Plusia gamma.

Scale: 1 unit = $\frac{1}{16}$ mm.

	Instar.										
	I.		II.		III.		IV.		V.		VI.
Headwidth series 1 . .	5·0		7·2		11·5		20·1		33·0		
,, ,, 2 . .	5·0		7·0		10·4		15·6		23·3		34·3
Progression factor :											
5-instar type . .		(1·45)		1·60		1·75		1·60			
6-instar type . .		(1·40)		1·49		1·54		1·49		1·47	

From Table IV it can be seen that series 1 had five instars whilst series 2 had six. The larvae following these series have been designated "5-instar type" and "6-instar type" respectively. It can also be seen that the difference between the sequences had become well marked by the instar III. The subsequent division of the head-width frequencies into the two instar types (figs. 8B, C) showed that there were approximately equal numbers in each (28 and 26 respectively).

The parallel crowded culture could not be analysed in the same direct way, as it was not possible to follow the successive widths for individual larvae. Furthermore the ranges of head-widths applicable to the various instars in the two instar types overlap, the clearest distinction probably being in instar IV

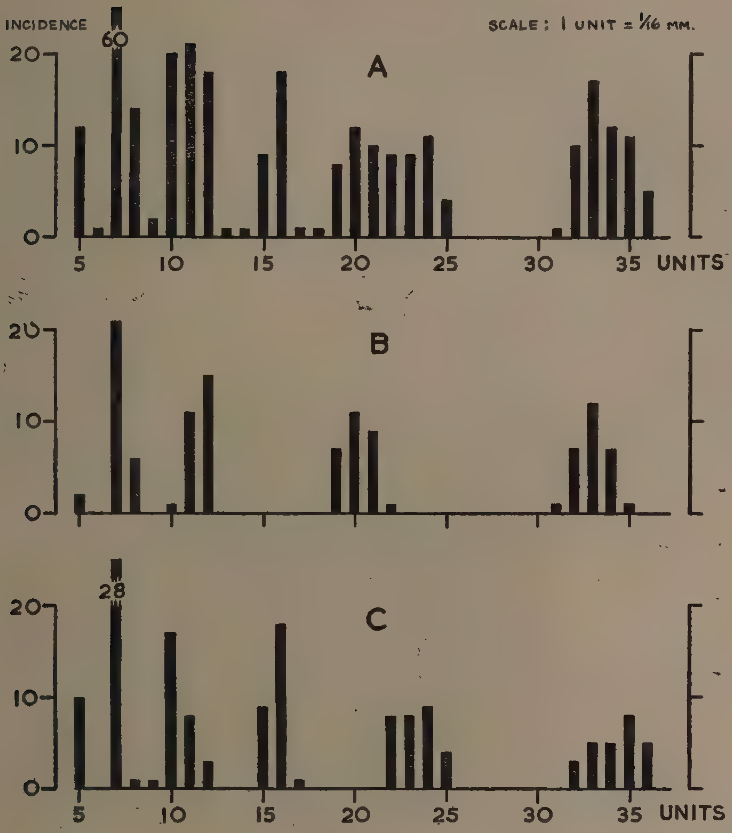


FIG. 8A.—The incidence of head-capsule widths within solitary cultures of *P. gamma* throughout larval life.

FIG. 8B.—The incidence of larvae having 5 instars in fig. 8A.

FIG. 8C.—The incidence of larvae having 6 instars in fig. 8A.

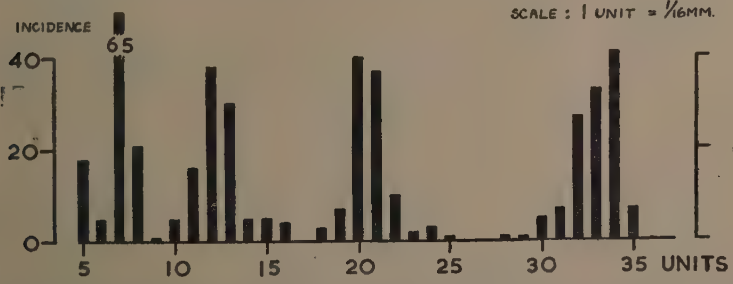


FIG. 9.—The incidence of head-capsule widths within a crowded culture of *P. gamma* throughout larval life.

of the 6-instar type. Thus larvae of the 6-instar type passed through a stage with head widths of 14–16 units, which afforded an estimate of their number, whilst those of the 5-instar type attained a head width of 18–22 units. As a result the 5-instar type formed the first major group to attain a head-width of about 33 units. The head-width frequencies for the parallel crowd to the solitary culture considered above is illustrated in fig. 9, from which the values obtained for the 5-instar type agreed closely with those given in Table IV. The number of 6-instar type larvae, however, were found not to exceed 16 in 154 larvae, or about 10 per cent. This is in marked contrast with the 50 per cent. of the solitary culture, and can therefore be attributed to the crowded condition in the first one or two instars. Thus in crowded conditions some larvae which would normally have developed through six-instars may be induced to develop through five.

Table IV shows that Dyar's progression factors for 5- and 6-instar types of the solitary larvae are fairly constant. In this culture there were, however, two larvae which moulted six times and therefore appeared to have seven instars (Table V). The progression factors, however, show a fairly constant value except for instars V, VI, and VII. If, however, the head-width for instar VII is compared directly with instar V a value of 1·50 is obtained, which is more in keeping with the progression values for the earlier instars. From this then it would appear that these larvae have only had six true instars with a supernumery moult occurring in instar V.

Table V.—*Successive head-widths and progression factors of two solitary larvae of* Plusia gamma.

Scale: 1 unit = $\frac{1}{16}$ mm.

	Instar.						
	I.	II.	III.	IV.	V.	VI.	VII.
Head-widths . . .	5	7	10	15	22	25·5	33
Progression factors		1·40	1·43	1·50	1·46	1·16	1·29

Examples also occur in the solitary culture of larvae starting to develop through the series of head widths typical of the 5-instar type until instar IV, after which they moult twice more, having head-widths typical of instars V and VI of the 6-instar type larvae (Table VI).

Table VI.—*Successive head-widths and progression factors of* Plusia gamma *larvae changing from a five-instar series to a six-instar series.*

Scale: 1 unit = $\frac{1}{16}$ mm.

	Instar.					
	I.	II.	III.	IV.	V.	VI.
Head-widths . . .	5	7	11·5	19	25	36
Progression factor . .		(1·40)	1·64	1·58	1·32	1·44

The progression factors in Table VI show a marked fall after instar IV, but a comparison of the head-width of instar VI with instar IV would give a factor of 1·89, which would be very high for a normal growth function. Thus instar V was almost certainly a true instar, which means that in conditions of isolation the converse of the effects observed in crowding may apply, namely that 5-instar type larvae may develop through six instars.

These results have been confirmed in later cultures using a finer scale of measurement (1 unit $= \frac{1}{25}$ mm.). Although a better separation of the 5-instar type and the 6-instar type larvae was achieved, margins of overlap of the two series of head widths still occurred and the general picture was not altered, although larvae having seven instars have again been encountered.

A similar analysis was made of solitary and crowded cultures of *D. oleracea*. The results of this are summarised in Table VII, where it can be seen that for those larvae which had six instars the mean head-widths of both the solitary and the crowded cultures agree very closely. In the crowded culture there was no occurrence of forms having a head-width about 58 units, so that it appeared to consist entirely of forms having six instars. In the solitary cultures, however, approximately 50 per cent. of the larvae had seven instars, whilst one larva had eight, and an examination of the progression factors showed that these were probably true instars. It is interesting to note that the head-widths of those with seven instars do not begin to diverge from those with six until instar IV, whilst that with eight began to diverge in instar III. It will be recalled that this divergence in *Plusia gamma* began in instar III. An examination of the progression factors renders it unlikely that this effect is an artifact due to the scale of measurement used, in which case another problem exists here as to the factors concerned in regulating the number of instars and the manner in which this regulation is achieved. Since divergences of the kind mentioned are accompanied by a marked fall in the progression factors, why cannot the earlier higher factor of development be maintained in all the larvae?

TABLE VII.—*Series of successive mean head-widths and progression factors of the larvae of* Diataraxia oleracea.

Scale: 1 unit $= \frac{1}{25}$ mm.

	Instar.							
	I.	II.	III.	IV.	V.	VI.	VII.	VIII.
Mean headwidth:								
1. Crowded	9·5	14·2	21·4	33·6	49·4	71·6	.	.
Solitary	9·6	14·5	20·9	33·0	49·8	70·7	.	.
2. Solitary	10·0	14·3	21·5	32·3	46·3	58·5	76·5	.
3. ,, *	9	14	19	26	37	47	58	78
Progression factor:								
1. Crowded	1·50	1·51	1·57	1·47	1·45	.	.	.
Solitary	1·51	1·44	1·58	1·51	1·42	.	.	.
2. Solitary	1·43	1·50	1·50	1·43	1·26	1·31	.	.
3. ,, *	1·56	1·36	1·37	1·42	1·27	1·23	1·35	.

* Based on one larva.

1. The number of instars and the periods of pupation.

A basic difference between 5-instar type and 6-instar type larvae is reflected in the length of the periods during which pupation is taking place. An example of this in a solitary culture is illustrated in fig. 10. Analysis of this example shows that not only are the mean times of pupation of each type significantly different but so are the lengths of the pupation periods ($t = 8{\cdot}14$; $P < {\cdot}001$). Thus over the peak period two-thirds of the pupations take place within 5·3 days in the case of the 5-instar type but take 8·4 days in the case of the 6-instar type larvae. This latter value is conservative as 6-instar type larvae which had a protracted development, pupating at intervals over a further 30 to 40 days or which finally failed to pupate after an extended period, have not been taken into account. As this type of larval behaviour was never observed in 5-instar type larvae, it does seem that six or more instars is associated with a condition of lower metabolism as expressed in the rate of development of the 6-instar type larvae.

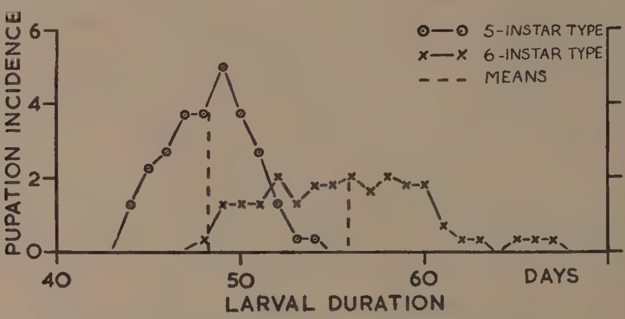


Fig. 10.—The pupation incidence of larvae of *P. gamma* having 5 and 6 instars throughout larval life (3-day running means).

2. The number of instars and the pupal weight.

In Table IV (page 564) it can be seen that there is a tendency for the head-width of the last instar of the 6-instar type larvae to be larger than that of the 5-instar type. The pupal weight can be directly correlated with the head-width of the last instar (fig. 11), so that it would be expected that cultures having a higher percentage of 6-instar type larvae would be heavier than those which had a higher percentage of the 5-instar type. It is for this reason that, when reviewing the mean pupal weights of solitary and crowded cultures (page 563), it was considered that the slight tendency for the mean of the solitaries to be heavier than the mean of the crowds represented an actual trend, because the solitary cultures have the greater percentage of the 6-instar type.

3. The number of instars and the genetic colour strain.

Following the colour selection in *P. gamma* referred to on page 554, the percentage of 5-instar type and 6-instar type larvae in both crowded cultures changed, so that by the 4th generation 5-instar type larvae only constituted 30 instead of 90 per cent. of normal crowded cultures and 5 instead of 50 per cent. of solitary cultures. The colour order of development within a crowded culture also changed, the light larvae which developed the quickest being virtually absent. In view of the fact that 5-instar type larvae developed quicker than 6-instar type, it seems reasonable to associate the former type with light larvae. This association would appear to be further confirmed by the fact that 6-instar type larvae have been observed to develop the darkest colours. However, there is insufficient evidence to draw the conclusion that the number of instars is genetically controlled ; in fact evidence to be discussed later seems to indicate that this is not so.

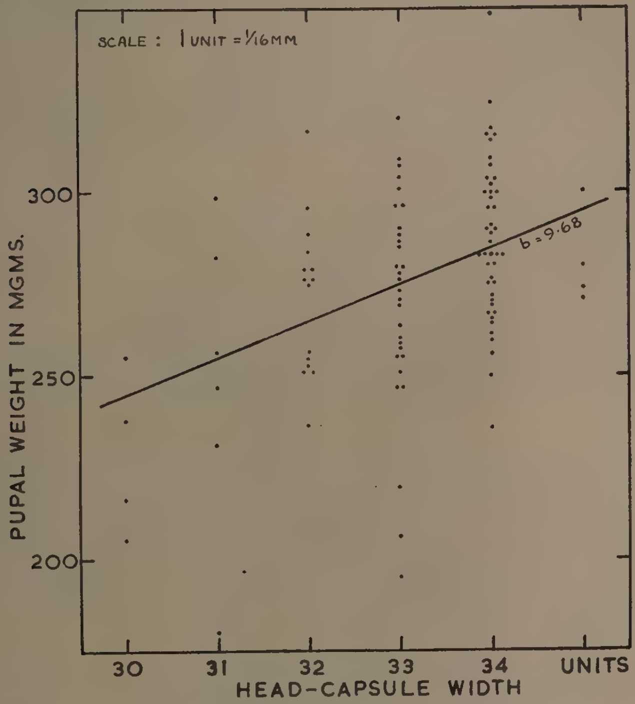


Fig. 11.—The correlation between the head-capsule width of the last instar and the pupal weight in *P. gamma.*

Population Density and the Larval Growth Rate.

The fact that crowded cultures develop more rapidly than do the parallel solitary ones can now be reconsidered from the point of view of the different composition of 5-instar type and 6-instar type larvae. Obviously since the crowded cultures had a higher percentage of the more rapidly developing 5-instar type larvae, it is to be expected that they would develop more quickly. How far this factor may operate can best be seen in an example given in Table VIII.

Table VIII.—*Mean larval duration and the number of instars in solitary and crowded cultures of* P. gamma.

Culture.	Instar type.	Per cent. composition.	Mean duration.	Total mean duration.
Solitary . .	5	55	48·3 days	51·6 days
,, . .	6	45	55·9 days	
Crowded . .	5 and 6	100		41·7 days

This table shows that the crowded culture took 81 per cent. of the duration of the solitary cultures with a difference of 9·9 days. Had the solitary cultures had the same composition as the crowd of 85 per cent. of the 5-instar type instead of 55 per cent. the total mean duration would have been 49·4 days. A difference however, of 7·7 days still remains unaccounted for. This difference must represent the net effect of a faster rate of development within the instar types in a crowded culture. Does this faster rate of development apply equally to both instar types in a crowded culture?

By following through the development of the instar types, in the example given, mean durations of 40·8 and 49·0 days were determined for the 5- and 6-instar types respectively. This shows the difference between the mean durations of the two instar types in this case to be 8·2 days. Had the faster rate of development applied equally to these two types the difference would have been proportionately less (6·4 days) than that of 7·6 days observed in the solitary culture. It appears therefore that the rate of development of the 5-instar type was the more affected by crowding.

To summarise the effects observed so far: crowding induces a more rapid development throughout the culture, associated with which is a higher incidence of larvae having five instars. Although faster than the solitary equivalents, the rates of development for the two instar types do not appear to be increased in similar proportions, the slower ratio being associated with larvae undergoing six instars.

An attempt was made to determine at what instar the faster rate of development first appeared, and also to obtain some information on the nature of its operation by means of an experiment the setting up of which is described on page 557. The object of the experiment was to compare the durations of the instars in the parallel lines, and at the same time to assess the effect of the condition of culture in instars I–III in relation to that in the remaining instars. The instar durations are summarised in Table IX.

TABLE IX.—*Mean instar durations in* P. gamma *in changed conditions of culture* (*described on page* 557).

	Instar.					Mean total
Line.	I.	II.	III.	IV.	V and VI.	duration.
1*	.	.	.	7·2	16·9	44·2
2	7·2	6·0	6·2	6·0	16·5	41·9
3	6·8	5·8	7·8	5·9	15·7	42·0
4	6·6	4·4	5·5	6·0	16·3	38·8
5	7·1	4·3	5·2	5·4	15·0	37·0

* As line 1, 2 and 3 were all solitary until instar IV no record of instar growth was kept for line 1 until this instar.

In instar I lines 2 and 3 were solitary whilst 4 and 5 were crowded, and it can be seen from Table IX that with means of 7·0 and 6·9 days respectively no effect has been produced on the instar duration by the condition of culture. In instar II, however, it is readily apparent that the crowded cultures were developing more rapidly, taking 1·5 days (or 25 per cent.) less than the solitaries. In instars III and IV the change of conditions was beginning to take effect such that the newly crowded lines 2 and 3 developed faster than the solitary control (line 1), whilst the newly isolated line 4 was slower than the crowded control (line 5). Little comparison can be made between the durations for the remaining instars as the durations of the different instar types were not known.

The total effects of the condition of culture in the different periods of larval life are summarised in Table X and fig. 12. From Table X it can be seen that in the time of 19·4 days taken for 50 per cent. to reach instar IV in the solitary condition there was good agreement in lines 1 and 2; the higher value of 20·3 days in line 3 was due to a temporary cessation of moulting into instar IV immediately following the change to a crowded condition.

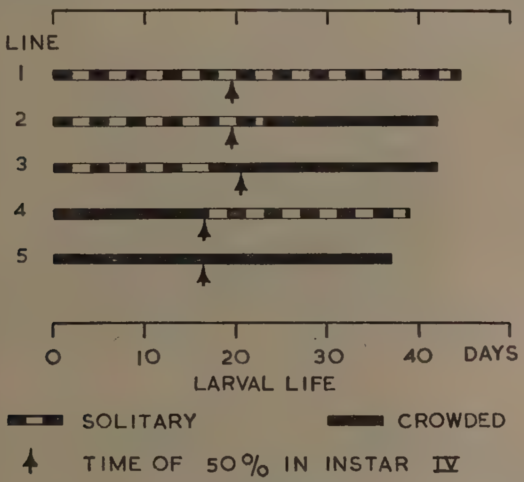


Fig. 12.—The effect on the larval duration of reversing the conditions of population density in parallel solitary and crowded cultures of *P. gamma*. (For details see text.)

Table X.—*Mean durations of larval development before and after change of condition of culture.*

Line.	Days for 50 per cent. to reach instar IV.	Total days to pupation.	Days from 50 per cent. in instar IV to pupation.
1	19·3	44·2	24·9
2	19·4	41·9	22·5 } 22·1
3	20·3	42·0	21·7
4	16·5	38·8	22·2
5	16·5	37·0	20·5

The period taken to reach pupation after 50 per cent. had reached instar IV was 24·9 days for line 1, whilst line 5 took 20·5 days or 82 per cent. of the former time, the crowded culture thereby taking for its complete larval development 84 per cent. of the time taken by the solitary cultures. From this it appears that the shorter duration of the crowded culture is the result of an effect produced evenly throughout larval life, but it has been shown (page 570) that there was no difference in the durations of instar I, and (page 569) that up to one-quarter of the total difference of duration of larval development could be due to different proportions of 5-instar type and 6-instar type larvae in the two conditions of culture, the effect of the additional instar becoming apparent in the later stages of development. Thus crowding may be expected to produce a greater effect in the early stages of development.

Although the time taken from 50 per cent. instar IV to pupation of the newly crowded lines 2 and 3 was less than that of the solitary line 1, it was still greater than that taken by the constantly crowded line 5. Therefore crowding in the later period can result in a more rapid development but the effect may not be so great as that produced in conditions of continual crowding, presumably due to a residual effect being carried over from the early stages of development in the latter. The existence of this residual effect seems to be borne out by line 4, which took less time for this later period after being changed to a solitary condition than did the solitary control. The fact that the time for line 4 was greater than the time for the crowded line 5 indicates that the rate of development in line 4 as induced by its earlier condition of crowding decreased after that condition was removed.

From these considerations we may conclude that the condition of culture in the first two instars was of the greatest importance, the maximum rate of development appearing in the second instar in a crowded culture. Although this rate decreases gradually throughout larval life, a degree of the effect produced by the earlier conditions was carried forward through each instar.

POPULATION DENSITY, THE FOOD-PLANT AND LARVAL DURATION.

When breeding parallel crowded cultures of *P. gamma* on different food-plants marked differences were observed in the rates of development. The results obtained with three of these plants for both crowded and solitary cultures are given in Table XI.

The solitary and crowded cultures were bred at different times so that no direct comparison can be made between them.

In the solitary cultures a comparison of the total mean times of instars I–IV shows that there was very little difference between the various food-

TABLE XI.—*Mean durations of larval development on different food-plants in relation to the condition of culture.*

Food-plant.	Condition of culture.	Per cent. composition.		Duration of instars.		Mean total duration.
		5-instar type.	6-instar type.	I–IV.	V and VI.	
Mustard . .	Solitary	20	80	21·5	.	.
Dandelion . .		73	27	20·3	.	.
Dock . .		0	100	22·2	.	.
Mustard . .	Crowded	50	50	23·7	10·4	34·1
Dandelion . .		97	3	17·6	8·1	25·7
Dock . .		53	47	21·9	13·2	34·1

plants, Dandelion being 6 per cent. faster than Mustard whilst Dock was 3 per cent. slower. In the crowded culture, however, up to instar IV Dandelion was 26 per cent. faster than Mustard whilst Dock was 8 per cent. faster. Their whole periods of larval duration still show Dandelion to be 25 per cent. faster than Mustard whilst Dock did not differ from the latter. Thus the faster rate of development on Dandelion is much increased by crowding.

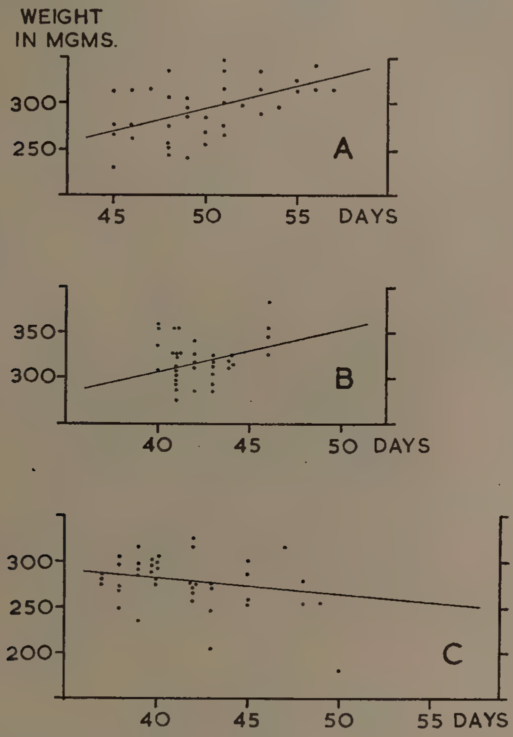


Fig. 13.—Correlations between larval durations and pupal weights in *P. gamma*. (For details see text.)

Fig. 13a.—A typical solitary culture with a colour range of grades 1-5.

Fig. 13b.—The light-coloured forms only of colour grades 3–5 in a crowded culture of moderate density.

Fig. 13c.—The dark coloured forms of colour grades 10–14 in a crowded culture of a higher density than b.

These results show that the effect of crowding in inducing a faster rate of development is not a constant independent of the food-plant.

From Table XI it can be seen that the highest percentage of the 5-instar type occurred in larvae having the most rapid rate of development such as the crowded culture on Dandelion, whilst the solitary culture on Dock, which was the slowest to develop, had none of this type. From these and earlier considerations it appears that the differences in the instar type composition on the various plants could probably be attributed to the physiological system governing the rate of development which has been shown to be affected by the nature of the food.

LARVAL DURATION AND PUPAL WEIGHT.

When the pupal weights of solitary larvae in a culture of *P. gamma* were compared in terms of the larval durations it showed that a positive correlation existed between the length of larval life and the pupal weight. This meant that there was a tendency for larvae having a longer period in the larval stage to attain a greater size as reflected by the pupal weight. A typical example is illustrated in fig. 13A, where it can be seen that the pupal weight was increasing by approximately 3½ mg. for each additional day of larval life.

An analysis of the pupal weights in crowded cultures of about 40 larvae per litre showed that whereas the light-coloured forms (grades 1–5) produced similar positive correlations to that occurring in solitary cultures, the correlations of the dark-coloured forms (grades 10–14) were generally slightly negative. In crowded cultures at higher densities the correlations for the light forms were only slightly positive, or even negative, whilst those for the dark forms became significantly negative. An example of the positive correlation of light forms in a culture at the lower density is given in fig. 13B, whilst fig. 13C illustrates the negative correlation of the dark forms at a higher density.

These considerations show that larval crowding affects the general pattern of development in terms of the final weight of the individual. From the fact that the dark forms were affected in crowded cultures at the lower densities, it seems that a fundamental difference may exist between the physiological responses of the light- and dark-coloured forms to the condition of crowding. Such a difference, however, is probably largely a matter of the degree of the response, as at higher densities the light-coloured forms were also affected. In view of this, any relationship between the effect produced in the dark form and the production of the colour is unlikely to be a simple one.

THE EFFECT ON THE SPECIFIC GRAVITY, FAT AND WATER CONTENT OF INDIVIDUAL LARVAE.

A crowded culture of 50 larvae of *P. gamma* was set up simultaneously with 50 solitary cultures on Agricultural Mustard. As the larvae reached the pre-pupal stage and ceased feeding they were removed for specific gravity determination and subsequent analysis. The specific gravity was determined by weighing individual larvae in air and distilled water. The larvae were then killed with chloroform and two short slits in the skin were carefully made, one in the anterior and the other in the posterior region of the ventral surface. Following this the larvae were dried ventral surface upwards either in a ventilated oven at 70° C. or in a desiccator (subsequently no differences in the results were observed between these two methods). The dry weights of the larvae were determined, and before extracting the fat with ether in a soxhlet[2], the individual larvae were wrapped in a marked cigarette paper. The process of extraction was maintained for three days after which the larvae were oven dried at 70° C. and reweighed. From these weighings the water and fat contents were determined as percentages of the original larval weight. These results are summarised in Table XII.

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[2] An apparatus for extracting substances by refluxing the material in boiling solvent.

TABLE XII.—*Mean specific gravity and mean fat and water content of* P. gamma *larvae.*

	Specific gravity.	Sp. gr. range.	Per cent. fat.	Per cent. water.
Solitaries . .	1·045	1·034–1·057	4·0	82·2
Crowd . .	1·048	1·041–1·055	4·9	81·5

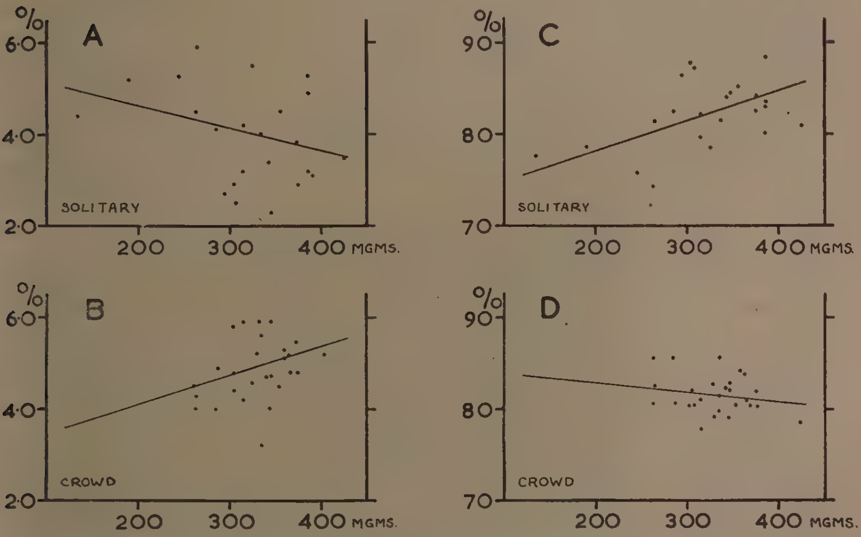

FIG. 14A and B.—The relation between the larval weight and the percentage fat content in *P. gamma* in solitary and crowded cultures respectively.

FIG. 14C and D.—The relation between the larval weight and the percentage water content in *P. gamma* in solitary and crowded cultures respectively.

The difference between the mean specific gravities of the two conditions of culture was slight and not significant. The solitaries were, however, the more variable, as can be seen in the specific gravity range in Table XII. The table shows that the mean percentage fat content of the crowds was greater than that of the solitaries. The mean percentage water content, on the other hand, was less in the case of the crowd but not significantly so.

The percentage fat content was not only less in the solitaries but decreased with increasing larval weight. This is shown by the negative slope of the regression line in fig. 14A, where an increase of weight of 189 mg. was correlated with a decrease of 1 per cent. fat content. In the crowd the slope of regression line was positive, with an increase of 180 mg. weight being correlated with an increase of 1 per cent. fat content (fig. 14B). The percentage water content, too, shows that crowding reverses the trend of the correlation with larval weight. The solitaries with their slightly higher water content showed an increase of 1 per cent. being associated with an increase of 30 mg. larval weight (fig. 14C). The crowd, however (fig. 14D), showed a decrease of 1 per cent. for an increase of 100 mg. larval weight. This latter correlation was the only one of the four considered which was not significant.

By considering figs. 14A, 14C, it can be seen that whilst with increasing weight in the solitaries the percentage fat content is falling, the percentage water content is rising. The complete reversal of both these observations by crowding shown in figs. 14B, 14D is therefore interesting.[3] As there is no correlation between the specific gravity and the larval weight for either the solitaries or the crowd it seems that the effects of the changes of fat and water content are too small to have much effect on the specific gravity.

Mortality (*P. gamma* and *D. oleracea*).

An analysis of the mortality in some 30 cultures shows that its incidence in the solitaries tends to be higher than in the crowds. Naturally there is a considerable degree of variability: the solitaries ranging from 12 to 90 per cent. about a mean of 47 per cent., whilst the crowd vary from 2 to 52 per cent. about a mean of 28 per cent. Certain factors such as the adverse conditions of winter affect both solitaries and crowds alike, but other factors are more closely associated with the conditions of culture. Thus cannibalism may rapidly reduce numbers in the crowds, whereas the solitaries are not subject to this hazard. The effects of disease too may be much more drastic in crowded cultures if it is not generally carried by the food-plant. The development of the solitaries, however, was frequently much protracted, and they often failed to complete it. In the case of autumn cultures this often resulted in the solitaries experiencing the adverse conditions of winter, which slowed up their development still further whilst the parallel crowded culture had already reached the pupal or imago stage.

In the solitaries the mortality occurred chiefly amongst those larvae having 6 instars which were the slower to develop. In the case of *P. gamma* larvae feeding on Dandelion, where development was the most rapid and the incidence of 6-instar type was minimal for both solitary and crowded cultures, the mortality was also minimal. From these considerations it does appear that conditions which lead to rapid development such as moderate crowding tend to keep the mortality to a minimum. With intense crowding, however, the mortality may be expected to rise again; thus in two crowds on Mustard there was 47 per cent. mortality in the culture of 200 larvae whilst there was only 18 per cent. in the culture of 60 larvae.

III. EFFECTS ON THE BEHAVIOUR.

The General Pattern of Behaviour.

Behaviour may be regarded as the outward expression of the ability of an organism to respond to its internal and external environments. The prevailing pattern of behaviour of an organism may therefore be considered as the exhibition of those responses being evoked at the time. Thus a change of behaviour involves a change in the nature of the response, whereas a change of the pattern can be regarded as being the result of involving other responses.

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[3] The reversal effect in the crowd was not attributable to the effect of crowding on the relationship between the larval duration and the pupal weight previously considered on page 574, as the correlations for these latter factors in the solitaries and the crowd were both positive.

When compared with the solitary condition crowding represents a change of environment and accordingly may lead to a change in the pattern of behaviour without necessarily involving a change in the basic behaviour. For example, the larvae of *P. gamma* in a crowded culture showed frequent avoidance reactions to other larvae and also warding off movements with the head and anterior region of the body associated with regurgitation which was never shown by the solitary larva in its environment. That this represents only a change in the general pattern of behaviour is shown by the fact that the solitary animal when put in with a crowd then showed these responses. Naturally other differences of the behaviour pattern of this type occurred between solitary and crowded cultures, but the most striking was the general impression that whereas the solitary larva was relatively immobile, larvae in crowded cultures were more inclined to restlessness. A higher level of activity in crowds would not be surprising, as it is probable that the environment of crowded larvae initiates extra responses.

POPULATION DENSITY AND THE LEVEL OF ACTIVITY.

In view of the apparent differences in general activity noted above experiments were set up which would determine whether these differences really existed, and if so whether they truly represented a change of behaviour. For this purpose larvae of *P. gamma* were bred as solitaries and in crowds of 12 larvae per cage. The hatching of the eggs for the crowds was delayed for 3 days by cooling, so that the development of the larvae in the solitary and crowded condition would be comparable by the last instar. The density of 12 larvae per cage was maintained throughout the breeding period by reduction of the number of separate crowds.

During the period when a fair proportion of both the solitary and crowded larvae had reached the last instar, 12 larvae from each condition of culture in a comparable stage of development in either of the last two instars were selected, care being taken to avoid larvae which were approaching the moulting period or the pre-pupal period. The 12 larvae of the crowd and the 12 solitary larvae were marked with two coloured spots for easy and rapid identification. Observations were then made at 10-minute intervals over a period of 12 hours and the behaviour of each larva in the 13 cages was simply recorded as follows:

F = feeding including masticatory movements.
A = any form of activity not recorded as feeding.
R = complete immobility regarded as resting.

The recording thermograph showed that the temperature remained constant within 1° C. throughout these experiments.

An analysis of the results of an experiment involving 7 hours of daylight and 5 hours of night showed no significant difference between day and night. The results of the experiments are given in Table XIII expressed as percentages based on the total of 1728 occasions when observations were made in each condition of culture.

TABLE XIII.—*Summary of behaviour as observed at* 10-*minute intervals expressed as percentages.*

Behaviour.	Normal condition.		Reversed condition.	
	Solitaries.	Crowds.	Solitaries.	Crowds.
Feeding	18·9	24·0	13·4	14·7
Active	2·4	10·8	9·9	11·8
Resting	78·7	65·3	76·7	73·5

Assuming that these results reflected the total behaviour over the period of the experiment, 13·4 per cent. more of the time was being spent resting by the solitaries than by the crowds. This means that the crowds were generally more active than the solitaries. Furthermore, it can be seen that only a small part of this increased activity was devoted to feeding; the crowds spent just over a quarter as long again feeding as did the solitaries. Much more striking is the fact that the crowds were active apart from feeding, more than four times as much as were the solitaries. This could account for the impression of a greater restlessness in the crowds. This activity on the part of the crowds included locomotion, swaying movements with the anterior region of the body (possibly exploratory movements) and irritation reactions between touching larvae. The next set of experiments were designed to determine how much of these differences represented changes in behaviour.

The experiments were set up and carried out in a similar manner to that just described, using the same larvae, except that for the duration of the experiment the 12 solitary larvae were crowded together and the 12 larvae of the crowd were isolated in separate cages. The results of this reversed condition of culture are given in Table XIII. It can be seen that the crowded larvae when changed to solitary conditions still spend less time resting than normal solitaries (73·5 per cent. against 78·7). On the other hand they were resting longer than their own normal of 65·3 by 8·2 per cent. This would mean just over half of the greater activity of the crowded over the solitary cultures represented simply a change in the pattern of behaviour. Although the mechanical aspect of crowding produced a change of 8·2 per cent. in the crowded larvae, in the solitary under reversed conditions of culture there was only a decrease of 2·0 per cent. in the resting time when compared with their normal. This indicates that the crowded larvae were probably more responsive to the condition of crowding than were solitary larvae.

The crowded larvae when in reversed conditions showed that feeding time fell by 9 per cent. whilst the time engaged in non-feeding activities remained much the same. This could mean that crowding leads to a change of behaviour involving non-feeding activities, whilst the mechanical aspects of crowding induce feeding. The solitary larvae in the reversed condition, however, showed a marked increase in the non-feeding activity largely at the expense of the feeding time. In this case it would appear that the more immediate effect of crowding is to reduce the feeding time presumably by mechanical disturbance.

Thus crowding may lead to two distinct changes in behaviour. These experiments have shown that crowding produces a change of behaviour reflected in a higher level of activity which more probably involves non-feeding movements. It also seems not improbable that whereas the mechanical aspects of crowding may act as a stimulant to feeding activity in crowded larvae, it has the reverse effect amongst solitary larvae. From these suggestions it is obvious that a further examination of this problem is necessary, as the observations have been made on the gross overall effects, and it is quite possible that neither of these changes of behaviour would be as direct and simple as they may first appear.

IV. CONCLUSION.

Discussion.

In the field the larvae of certain species of Lepidoptera tend to be solitary and such conditions can be reproduced in the laboratory. In others which live in close or loose aggregations, the population density that may be considered normal to the species is not known. This leads to difficulties in interpreting the result of an experimental condition of isolation or crowding as a departure from the normal. Thus a given difference between solitary and crowded cultures may represent the result of extra stimuli occurring in the crowd, or the absence of stimuli normal to the species occurring in conditions of isolation. It has not been possible therefore to associate the results obtained with the relation of the individual species to its natural environment.

Since many of the experiments have been of necessity limited to one or two species a complete comparison of all the species originally listed cannot be made. From the results obtained it appears that marked differences in the effects of population density may occur between species. Thus for example *P. brassicae* showed no obvious colour response to a crowded condition, although the rate of development was increased. *S. pavonia*, however, showed a clear colour response whilst the effect on the rate of development was slight. In contrast both *P. gamma* and *D. oleracea* exhibited both of these effects.

Amongst those factors involved in the response of larvae to a crowded condition of culture, that of the normal behaviour indigenous to the species is most possibly of prime importance. In the case of *P. gamma* it has been shown that sight is not the principal sense involved. Unless the sense proves to be one of smell, the effects must almost certainly be due to the close proximity of larvae or contact between them. If the larvae keep apart and are generally static they will interfere little with each other and the effect of crowding may therefore be negligible. If, on the other hand, the larvae are highly active, gregarious and possibly aggressive the effect of their proximity may be profound. The larvae in which the effects of population density have been observed generally conform with the latter group.

The manner in which melanization of the cuticle surface spreads progressively downwards from the tips of the spines suggests that the difference in melanization between solitary and crowded larvae is due to an ability of certain hypodermal cells of the former to inhibit the pigmentation of the overlying cuticle. As with most of the component structures of living organisms, the pigmentation of the hypodermis probably represents a state of equilibrium between simultaneous processes of synthesis and destruction. Many insect pigments certainly appear to be unstable and are extremely difficult to preserve *in situ*. Such a dynamic mechanism could allow colour changes throughout life as well as accounting for the range of colour variation normal to the species.

Although it has been shown that larval crowding may produce a colour change involving a darkening, other factors are known to affect the colour. In the case of locusts Husain and Mathur (1936*a*) showed that solitary hoppers bred in air containing 3 per cent. (by volume) of carbon dioxide had a typical gregarious type of coloration and they (1936) also showed that a higher level of activity in solitary hoppers enforced by mechanical action had a similar effect. Again, Plotnikov (1924) obtained gregarious forms amongst crowded hoppers bred in darkness. We obtained a similar result in caterpillars with the larvae of *P. gamma* (page 562), whilst Faure (1943, 1943*a*) showed that solitary larvae of *Laphygma exigua* Hübn. reared in semi-darkness on a black background and solitary larvae of *L. exempta* Walk. bred in complete darkness also produced dark forms. It seems that darkening is a common end-effect which results from a variety of disturbing conditions, of which crowding is one example.

However, in the case of *P. gamma* it has been shown that the food plant can affect the coloration. It seems unlikely that the larvae were simply responding to differences in the colour of the background, as the same mean larval colour was obtained in cultures feeding on plants of different colours. The effect of the plant therefore is possibly due to variations in the presence of one or more chemical substances in its leaves. The difference in colour between solitary and crowded forms may then be due to the fact that certain substances are metabolised differently in solitary and crowded conditions.

The effect of crowding on the rate of development is probably of considerable physiological significance. It certainly appears that the number of instars and the mortality are closely related to it. Klein (1932) found that with the higher temperatures and lower humidity of the summer months the larvae of *P. brassicae* underwent fewer instars. He therefore attributed the number of instars to the prevailing temperature throughout development. However, temperature acts in a similar manner to that of crowding and of the food plant in that they affect the rate of development and so may influence the number of instars.

Apart from differences in the numbers of instars the effect of crowding in accelerating the rate of development raises an interesting problem of the mechanism involved. Mosebach-Pukowski (1937) considered that a local temperature rise occurring within the closely packed colonies of *Vanessa io* and *V. urticae* accounted for the shorter duration of larval development occurring under these conditions. A similar view was taken by Wardzinski (1938) in his experiments with *Pieris brassicae* L., though his special conditions of feeding may have affected the results of the factors he studied. At least in the cases of *P. gamma* and *D. oleracea*, increased temperature due to proximity could not be the factor as the larvae do not lie side by side. Furthermore the temperature rise of $1\frac{1}{2}$ to 2° C. that Mosebach-Pukowski found necessary to induce solitary larvae to develop at the same rate as the crowded ones, is too large to be produced by extra activity in crowded cultures.

It has been shown that when larvae which have been crowded are later isolated their level of non-feeding activity is not markedly affected, whilst their total activity remains greater than that of normal solitaries. This greater activity is therefore presumably due to a physiological as distinct from a mechanical factor which has been carried over from the previously crowded condition. The development of the higher activity level and its associated physiological component throughout successive instars may originate from the simple mechanical effect of contact between larvae. Such contacts will certainly cause extra stimuli in the larval sense-organs and initiate extra responses over those experienced by the solitary larvae. This condition of stimulation may result in a higher level of nervous " tone " which, coupled with the effect of increased feeding and the mechanical effect of extra movement on the internal physiological processes, could affect the rate of development.

Grison (1948) found that the rate of increase in weight of crowded larvae of *Euproctis phaeorrhaea* Don. during the period prior to entering diapause was greater than that of solitary larvae. However, since the stages of development of the larvae are not given, it is not clear whether crowding induced a faster rate of development or involved the production of a relatively heavier larva.

Although in some of the experiments larval development has been considered in terms of the final weight, the results cannot be freely interpreted as being either advantageous or disadvantageous. What is of importance to the species is that it should survive and be capable of reproduction. Presumably a minimum developmental weight is necessary to achieve this, but the value of any excess weight is difficult to assess. The trend of the weights, however, may reflect the trend of the growth processes. It has been shown that within a crowded culture of *P. gamma* the non-pigment-producing forms tend to develop more rapidly than the dark pigmented larvae. Furthermore, at moderate densities the pupal weight increases with larval duration in the former case at about the same rate as in solitary cultures, whereas in the latter case the effect of the duration on the weight is reduced or even reversed. From the point of view of the weight it seems that the processes leading to pigmentation interfere with growth, and possibly at the same time reduce the rate of development. It has been observed that the greater the population density the more marked both these effects become.

Faure (1943, 1943*a*) considered the effects of his breeding experiments with *Laphygma exigua* and *L. exempta* in terms of phases. However, considerable confusion has developed in the literature as to the meaning of the term "phase" as reviewed by Key (1950). Accordingly the use of the term "phase" to describe the different forms obtained in lepidopterous larvae has been avoided. However, from the results obtained it can be seen that a number of the effects of the population density are parallel to similar effects that have been observed in locusts, as discussed in the following summary.

In both caterpillars and locusts there is a marked similarity in the colour response to crowding conditions with the production of dark forms. In neither case is the response absolutely uniform throughout a population, there being a degree of variation in the intensity of the response. As in *P. gamma*, *O. cruda*, *O. gothica* and others no locusts typical of the gregarious phase has ever been observed to develop in a simple solitary culture. The nature of the colour response has been found to vary from species to species both in Lepidoptera and Acrididae. In locusts Faure (1932) found that the presence of an abundance of fresh succulent food affected the green coloration of the solitary locust, but it is not possible at this stage to conclude that this is parallel to the effect of the food-plant on the coloration as has been observed in *P. gamma*.

In both groups the largest colour changes occur during the moulting periods. In *P. gamma* it was shown that with a change of condition the dark coloration was lost more rapidly than it could be built up ; and Faure (1923) made a similar observation on colour changes in the hoppers of *Locusta pardalina* Walk. A big difference, however, lies in the fact that the locust hatchlings of ph. *gregaria* parents are generally black whereas those of ph. *solitaria* tend to be green. No such difference has been observed in the newly emerged larvae of Lepidoptera.

In locusts the dark forms generally involve an extension of the black areas coupled with the development of yellow or orange pigment. In caterpillars this type of colour-darkening is frequently involved. In *S. pavonia* there is simply an extension of the black transverse bands: in *O. gothica* the chalk-white stripe changes to a bright yellow with the addition of a small amount of black; whilst in *O. cruda*, *P. gamma* and others, although the details of the colour changes associated with darkening are less clear, white is frequently replaced with yellow and there is an increase in black areas. Goodwin (1952) has made an extensive biochemical examination of locust pigmentation, and has found (1953) certain differences between the pigments of the light and dark forms of *Plusia gamma* from our experiments which were similar to those occurring between the phases of locusts. In locusts the dark areas due to melanin are an intense black, but in caterpillars they are often a dark brown. This may be due to the thin surface layer involved in the pigmentation of the larval skin.

The weight of solitary caterpillars appears to be greater than crowded ones: in locusts the greater weight of the ph. *solitaria* is quite marked. In caterpillars it has been shown that the effect of crowding on the development involves a reduction in the number of instars. Burnett (1951) states that 6 instars occurred in the ph. *gregaria* of *Nomadacris septemfasciata* Serv. in contrast to the 7 instars normally found in the ph. *solitaria*. As in caterpillars, the rate of development in locusts is slower in the solitary cultures (Chauvin 1941), and also there is a tendency for the development of some of the solitary hoppers to become protracted, frequently followed by death. The higher mortality which occurs in crowded locusts in experimental conditions is attributed by Uvarov largely to the lower degree of care per locust they receive when compared with that given to solitary cultures.

The analysis showing that there was a higher fat content and a lower water content in the crowded larva of *P. gamma* is in agreement with the determinations of Mathée (1945) of these substances in both locusts and two lepidopterous species. However, the later work of Cheu (1952) suggests that there are differences in the fat metabolism in the different phases of the adult locust which possibility has not yet been tested in the Lepidoptera.

In the early work on locusts, migration formed one of the major features of behaviour attributed to the ph. *gregaria*. Later observations of Ramchandra Rao and Bhatia (1939) and Ramchandra Rao (1942) inferred that ph. *solitaria* is also capable of migration over large distances. More recently the suggestion of Rainey (1951) that prevailing winds were possibly responsible for many apparent migrations throws some doubt on the previous evidence for their ability for true migration. From these considerations it can be seen that a relationship between the phase and migration in locusts is not so certain as at first it was thought to be. The colour responses in caterpillars do not appear to be related to a migratory tendency, for although *P. gamma* is a migrant, *S. pavonia*, *O. cruda* and others are not, whilst *P. brassicae*, which is also a migrant showed no colour responses.

Apart from the question of migration, other differences in behaviour between the phases in locusts also exist. The ph. *gregaria* hoppers are more active, and they demonstrate a marching behaviour not found in ph. *solitaria*. In caterpillars a higher level of activity has been shown to exist in crowded larvae of *P. gamma*, whilst the larval columns in the dark forms of the Southern Army Worms of Faure (1943, 1943*a*) may be analogous to the marches of the locust hoppers, but no appropriate experiments on their behaviour were carried out. This feature of greater activity in the crowded cultures raises possibilities of interesting physiological effects. With greater activity it may be expected that the spiracles are open for a greater period of time than in the less active solitary forms. This would permit a greater loss of moisture which generally can only be replaced by the water in the food. Thus to maintain a normal water metabolism it may be expected that crowded larvae will spend more time feeding, and this in fact has been observed in *P. gamma*. This in turn may be related to the differences observed in the fat and water contents.

Recently crowding has been observed to affect another fundamental aspect of locust behaviour. Ellis (1953, in the press) has shown that the tendency towards aggregation is higher in ph. *gregaria* hoppers, whereas ph. *solitaria* are more attracted by inanimate black objects. However, the attraction to ph. *gregaria* hoppers can be developed by ph. *solitaria* hoppers, and the response once acquired may persist for a considerable period in spite of continued isolation. From such observations a basis may thus be provided for a better understanding of the occurrence of crowding conditions in the field.

In locusts it is known that many of the effects of crowding in the hopper stages are carried over to the adult stage, but in Lepidoptera no effect has yet been observed in the adult. Although a study of this problem has not been undertaken, it can be appreciated that it may be of far-reaching effect in its general ecology. However, there is a major difference in the development of Orthoptera and Lepidoptera in that the former is hemimetabolic whilst the latter is holometabolic. Lepidoptera thus experience a quiescent pupal period of virtual isolation whatever their condition of crowding, and it might be expected that the imago will be accordingly affected.

From the foregoing it can be seen that the population density produces an extensive range of similar effects in both caterpillars and locusts. It therefore seems reasonable to conclude that the biological principles involved are the same whether or not the term "phase" is used.

This study must naturally lead to the question of the significance of these effects in the field. No direct approach on this problem has yet been made as the work has been exploratory in nature. However, a brief consideration suggests that the effects may be considerable. For example, crowding can induce a faster rate of development with fewer instars and a better synchronisation of development and lower mortality. The resulting pupal stage appears to be unaffected, and a better opportunity for mating is afforded by the subsequent simultaneous emergence of the adults. In favourable conditions in a multivoltine species these factors would operate in favour of a population build-up. In promoting an intensification of crowded conditions this reaction is unlike the many balancing reactions in nature which oppose a change of conditions. In locust studies a knowledge of the effects of population density has proved a valuable guide in the approach made to its ecology and control, but it now appears that this knowledge may be applied to a wider field of insect life.

SUMMARY.

Some effects of population density were determined by comparing solitary larvae with those bred in crowded cultures.

Ten species were used, seven of which showed differences in the larval coloration, the crowded larvae being generally darker than the solitary. The population density produced other effects in one of the three species that showed no colour response. The colour differences in three species that were examined were caused by variation in the pigmentation of the hypodermis and the cuticle. Pigment-carrying hypodermal cells were often enlarged, and appeared to be related to the darkening of the cuticle.

Solitary and crowded larvae frequently did not differ in colour until about the fourth instar. The light-coloured solitary larvae of *Plusia gamma* were darkest immediatly after each moult, and became generally whitened during the course of the instar; crowded larvae became much darker with successive moults, and the intensity of the colour also decreased during each instar but without associated whitening. When an alteration of the population density caused a colour change, most of the change occurred during moulting. The individual larvae in crowded cultures of *P. gamma* had widely different degrees of darkening, probably because the stock was not homozygous. The mean colour of a crowded population generally depended on the larval density. The darkening response, which was affected by the nature of the food-plant, was not dependent on the sense of sight.

Solitary larvae appeared to be slightly heavier than those in crowds.

Crowding increased the rate of development, the larval duration often being 80 per cent. of that of the solitary larvae. Up to one-quarter of the difference in time was due to the fact that crowded larvae generally underwent fewer instars. The number of instars is not genetically determined, but appears to be least when development is quickest. Other characteristics of crowded cultures which were associated with the fewer number of instars included a more simultaneous pupation, a lower pupal weight and a lower larval mortality. The nature of the food-plant affected the rate of development more in crowded than in solitary cultures.

The crowded larva had a higher fat and lower water content than the solitary larva.

The larval behaviour of the individual species appeared to be a most important factor. In *P. gamma* the crowded larvae were not only four times more active than solitary larvae but spent 25 per cent. more time feeding.

A further consideration of these points and others, together with a comparison of parallel effects observed in the phases of locusts, is given in the discussion.

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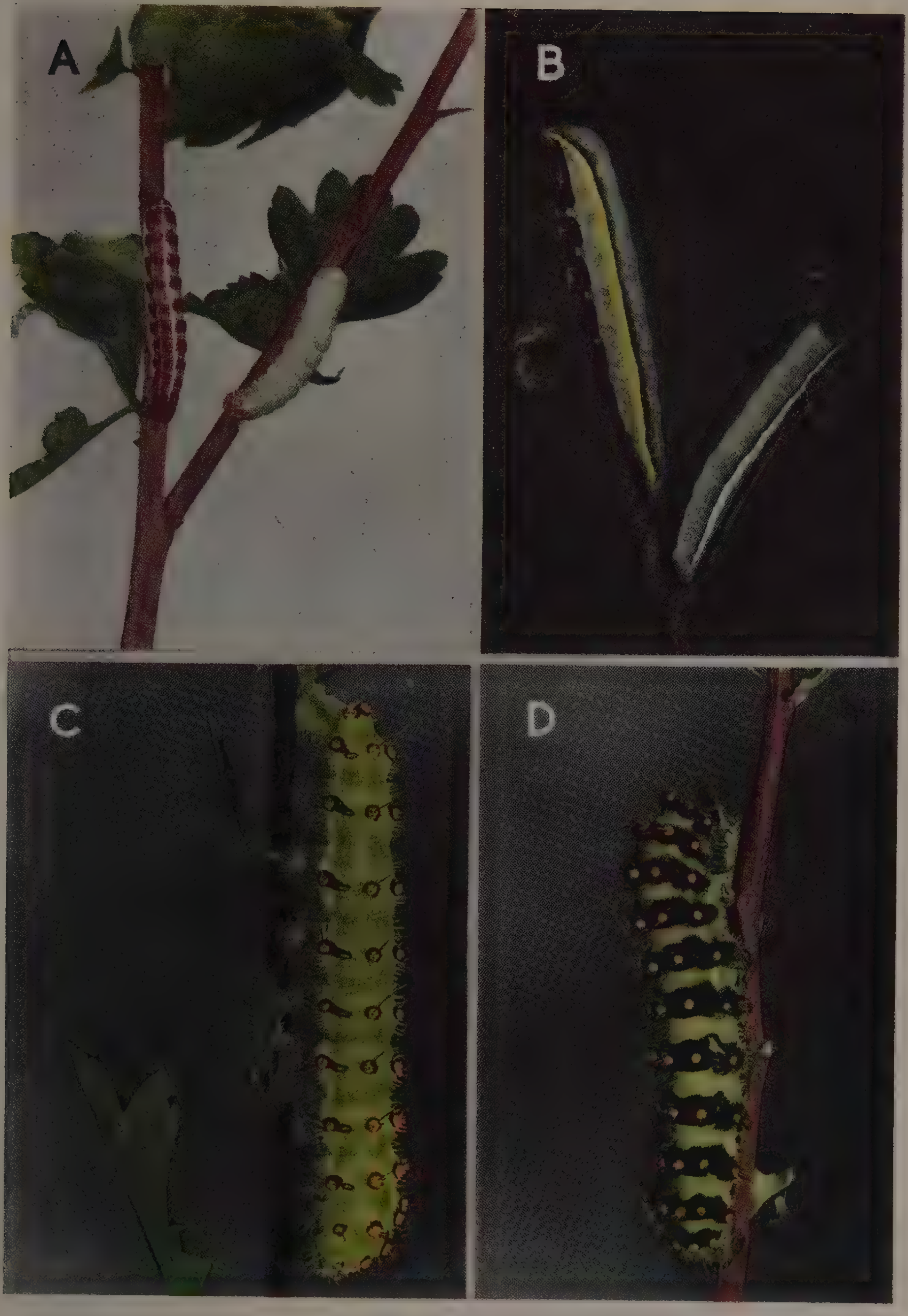
PLATE I.

Colour Differences Associated with the Population Density.

A. *Orthosia cruda* from crowded and solitary cultures left and right respectively.
B. *O. gothica* similarly from crowded and solitary cultures.
C and D. *Saturnia pavonia* light and dark extreme forms from solitary and crowded cultures respectively.



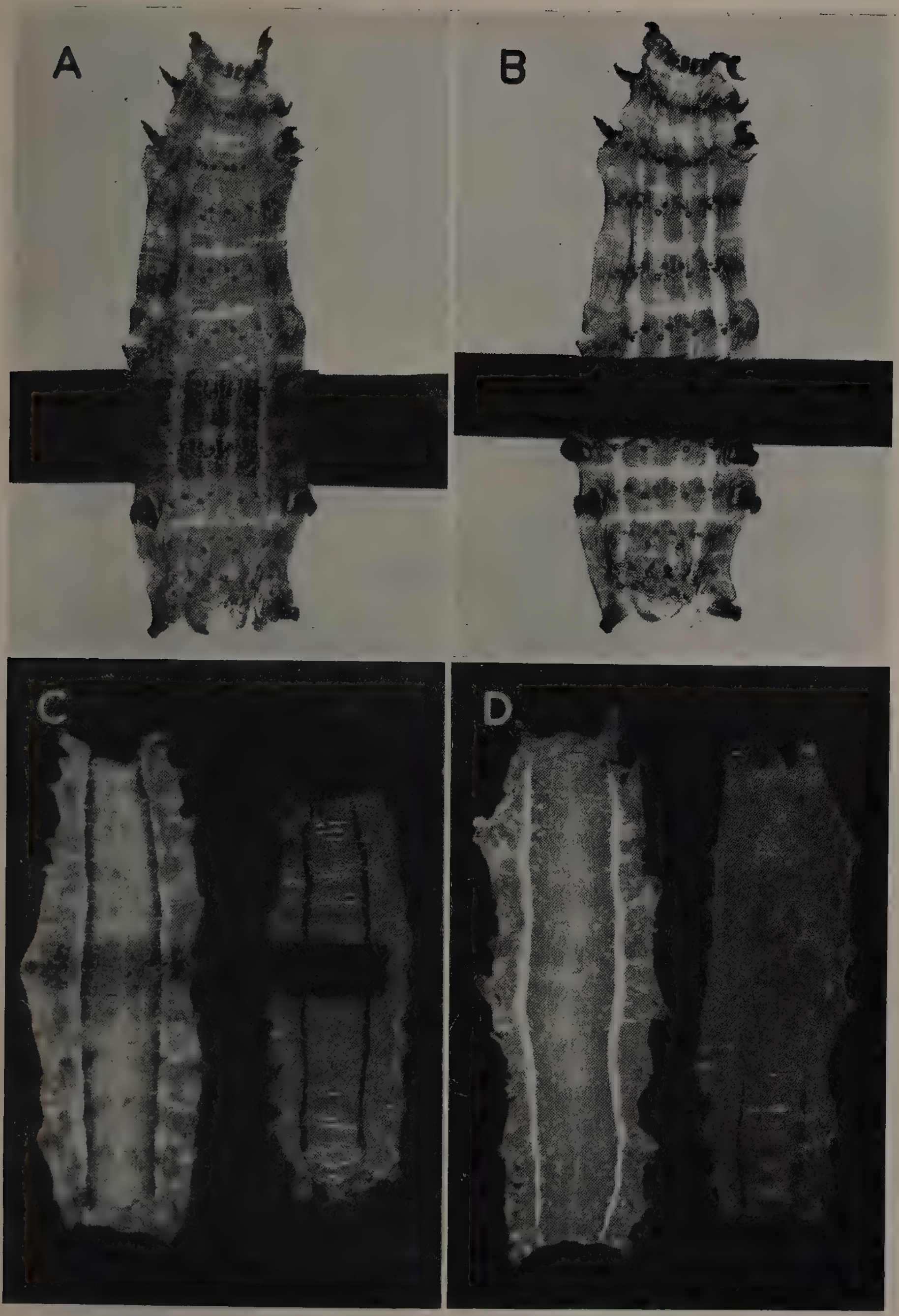
Colour differences associated with the population density.

D. B. Long.

PLATE II.

LARVAL DISSECTIONS SHOWING THE EXTENT OF THE DORSAL PATTERN IN THE HYPODERMIS AND THE CUTICLE.

A. *P. gamma.* Dark crowded form with the hypodermis intact.
B. *P. gamma.* The cuticle after removal of the hypodermis in A.
C. *O. gothica.* The crowded form before and after the removal of the hypodermis, left and right respectively.
D. *O. gothica.* The solitary form before and after the removal of the hypodermis.



Larval dissections in *P. gamma* and *O. gothica* showing the extent of the dorsal pattern in the hypodermis and the cuticle.

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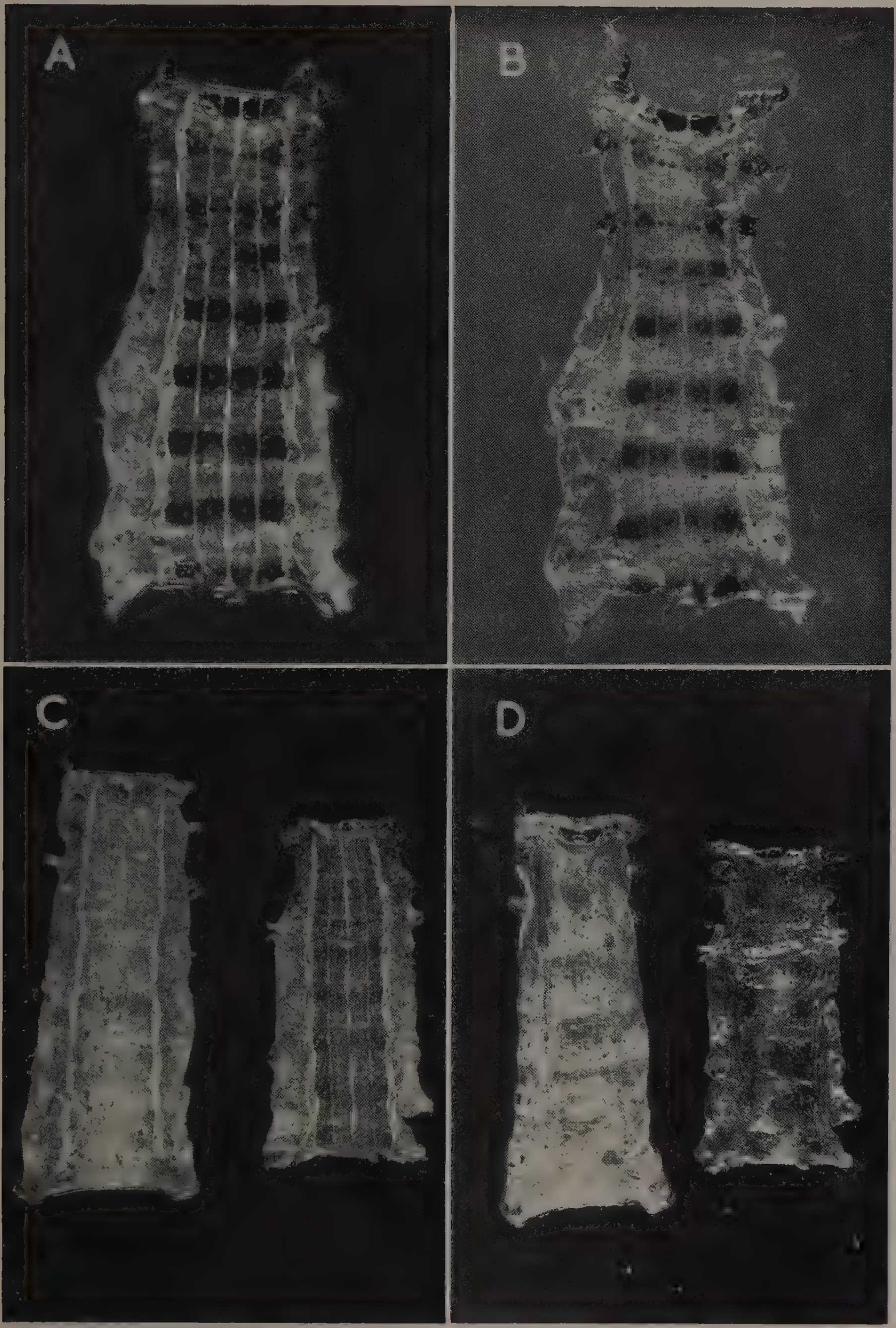
PLATE III.

LARVAL DISSECTIONS IN *O. cruda*, SHOWING THE EXTENT OF THE DORSAL PATTERN IN THE HYPODERMIS AND THE CUTICLE.

A. The crowded form with the hypodermis intact.
B. The cuticle after the removal of the hypodermis in A.
C. The solitary green and red forms (left and right respectively) with the hypodermis present.
D. The cuticles of the solitary forms in C.



Larval dissections in *O. cruda*, showing the extent of the dorsal pattern in the hypodermis and the cuticle.

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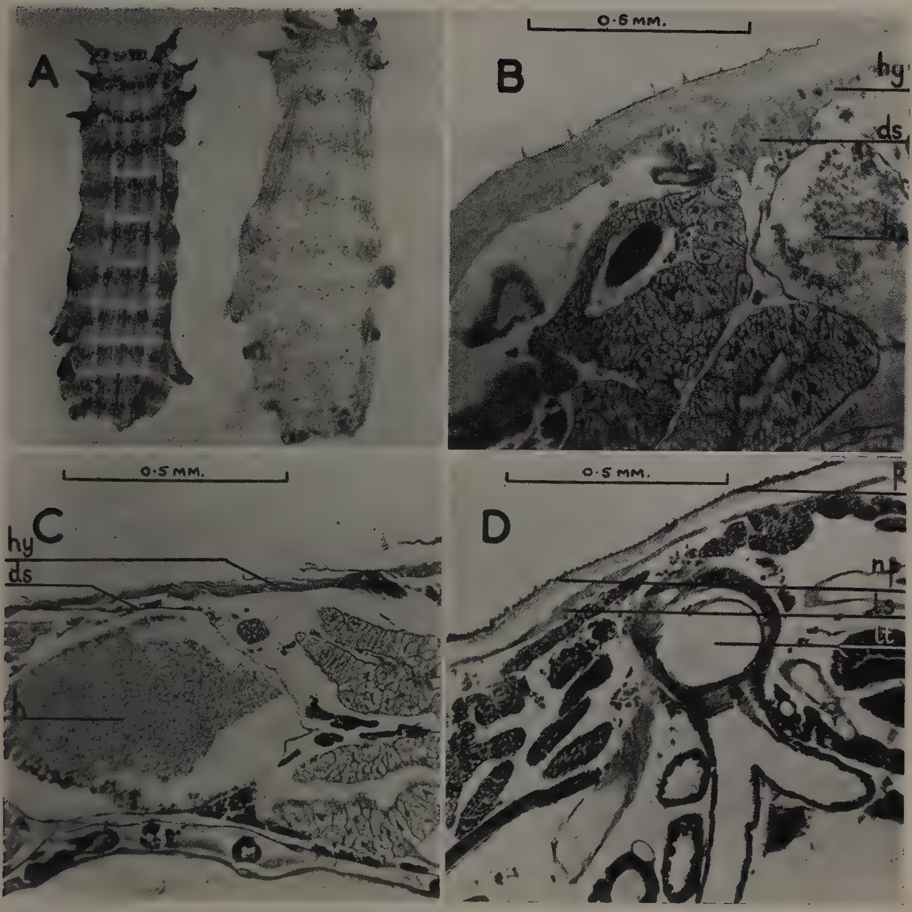
PLATE IV.

A. *P. gamma.* The cleared skins of dark crowded and solitary forms, left and right respectively.

Transverse sections.

B. *O. cruda.* Solitary red form showing the generally large hypodermal cells.
C. *O. cruda.* Solitary green form showing the generally small hypodermal cells.
D. *P. gamma.* Dark crowded form showing non-pigmented cuticle overlying the larger lateral stripe cells of the hypodermis :

ds, dorsal stripe cells ; *h*, heart ; *hy*, hypodermis ; *ls*, lateral stripe cells ; *lt*, lateral trachae ; *np*, non-pigmented cuticle ; *p*, pigmented cuticle.


A
B
0·5 MM.
hy
ds
C
0·5 MM.
hy
ds
gr
D
0·5 MM.
R
np
ts
tt

Cleared skins of *P. gamma* and transverse sections of *P. gamma and O. cruda.*

PLATE V.

Transverse Sections of Larval Cuticle.

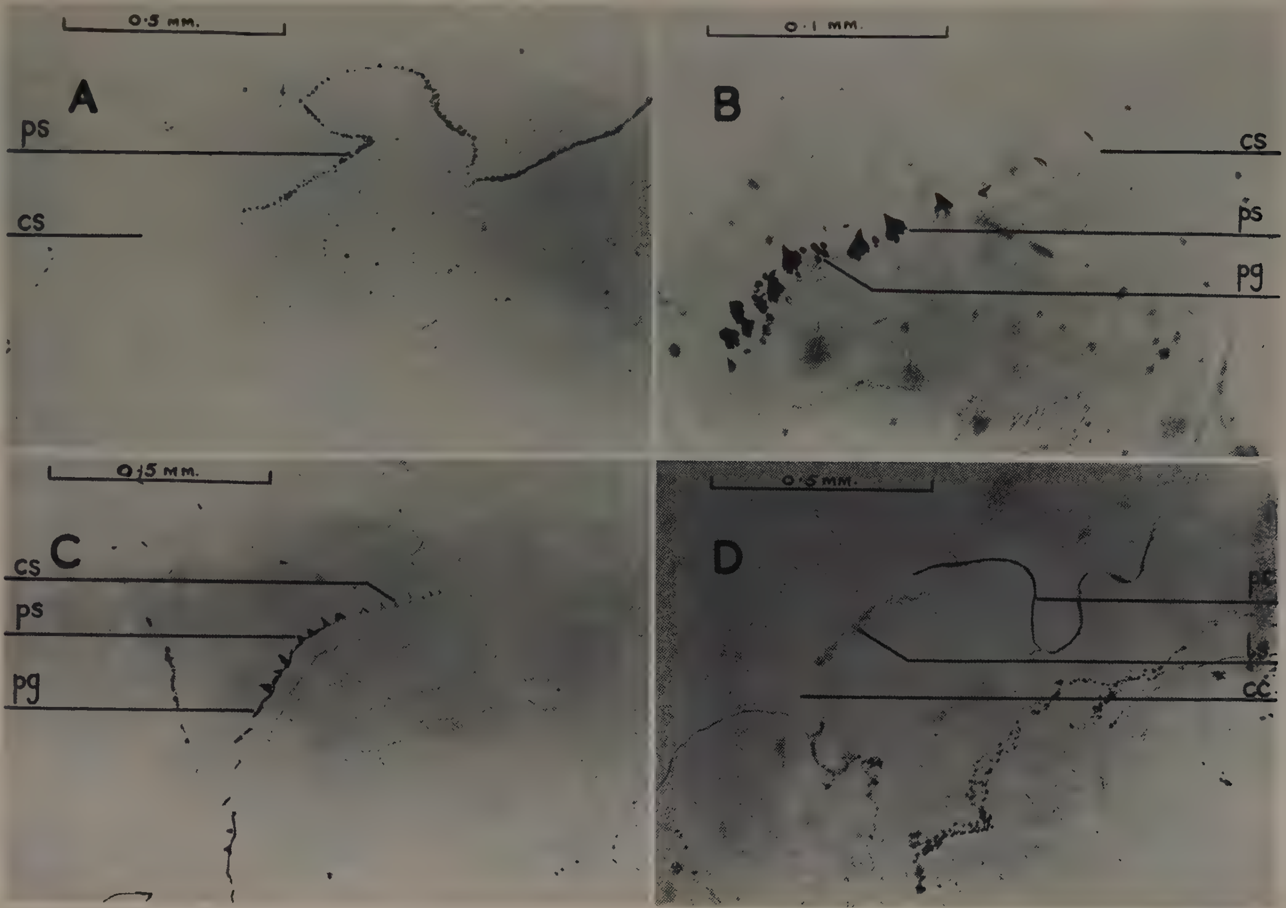
A. *P. gamma* showing the pigmented spines and the clear spines in the region of the lateral stripe.

B. *P. gamma* showing the buttressed spines with pigmentation spreading progressively downwards from the tip and the pigmented granules.

C. *O. cruda* showing clear and pigmented spines and pigmented granules.

D. *O. gothica* showing the evenly pigmented cuticle dorsal to the clear cuticle overlying the the lateral stripe hypodermal cells.

cc. clear cuticle ; *cs*, clear non-pigmented spines ; *ls*, lateral stripe cells of the hypodermis ; *pc*, pigmented cuticle ; *pg*. pigmented granules ; *ps*, pigmented spines.


0·5 mm.
A
ps
cs
0·1 mm.
B
cs
ps
pg
0·5 mm.
C
cs
ps
pg
0·5 mm.
D
pe
bs
cc

Transvere sections of larval cuticle.

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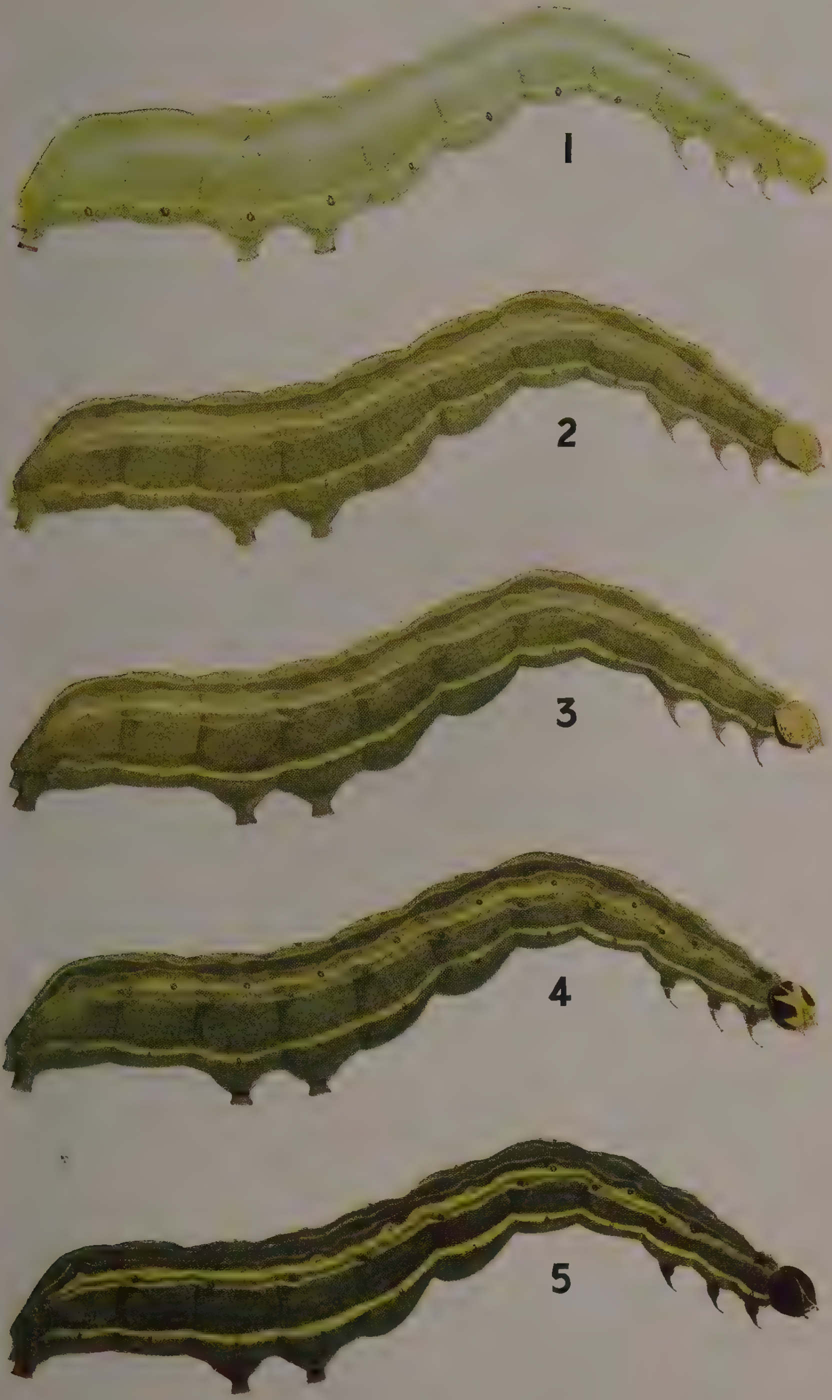
PLATE VI.

Colour Variations Occurring in *Plusia gamma*.
Numbers indicate Colour Groups.

The larval colours typifying the five major colour groups formed from fourteen successive grades :

Colour grade	1–3	4–5	6–8	9–11	12–14
Colour group	1	2	3	4	5

Colour group 1 is typical of solitary cultures, whilst colour groups 1–5 may occur in crowded cultures (for details see text).



Colour variations occurring in *Plusia gamma*.

D. B. Long.

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ERRATA.

p. 70, line 7. For "*Dyrinus*" read "*Dryinus.*"

p. 143, **Conclusions**. 1. line 3. For "in unnesessary" read "is unnecessary."

p. 206, line 2 from bottom. For "*Bioryhza*" read "*Biorhyza.*"

p. 245, line 16. For "*Lasiopssub rostatus*" read "*Lasiops subrostatus.*"

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